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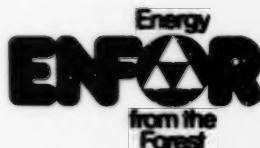
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**Nutrient Cycling in *Populus*:
A Literature Review
With Implications in
Intensively-Managed Plantations**

B. Bernier
Canada



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NUTRIENT CYCLING IN *POPULUS*:
A LITERATURE REVIEW
With Implications in Intensively-Managed Plantations

by

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PREFACE

In April, 1978, a number of countries within the International Energy Agency (IEA) decided to sign an Implementing Agreement (IA) for a program of research, development and demonstration on forestry energy. The work is implemented via Programme Groups and Cooperative Projects.

Work within the group for biomass growth and production has resulted in many reports which are being published in this series. The funds for the publication of these reports have been supplied by the Biomass Energy Project of the National Research Council of Canada, the Ontario Ministry of Natural Resources, and the Canadian Forestry Service.

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ABSTRACT

The increasing needs for forest tree biomass for pulp production or as a source of energy have raised much interest for dense plantations of poplars intensively cultured in short rotations. Because tree growth and nutrition are intimately linked, this review attempts to inventory and bring together published information on nutrient requirements by poplars and on nutrient cycling in natural stands and plantations of *Populus*. Available data on nutrient accumulation in tree biomass and in stems and branches are summarized, together with published information on nutrient translocation and uptake to meet nutrient requirements. Published data on nutrient return in litter-fall and throughfall and on nutrient release from the forest floor are presented. Based on literature data, simulated nutrient removals through harvest of stems and branches are presented for various rotation lengths and their potential consequences on maintaining site productivity are discussed in the light of nutrient budget considerations.

RÉSUMÉ

Les besoins accrus de biomasse forestière pour la production de pâte, ou d'énergie, ont soulevé un intérêt particulier pour les plantations denses de peuplier cultivé en taillis à courte révolution. Parce que la croissance des arbres est indissociable de leur nutrition, la présente revue tente d'inventorier et de rassembler les informations publiées sur les besoins en éléments des peupliers et sur le cycle des éléments dans les peuplements naturels et les plantations du genre *Populus*. Elle traite de l'accumulation des éléments dans la biomasse et, en particulier, dans les tiges et branches. Elle fait la synthèse des données acquises sur la translocation saisonnière et le prélèvement d'éléments pour satisfaire aux besoins des peupliers, de même que sur la restitution d'éléments par la chute de litière et la pluvio-lessivage, et sur la libération des éléments de la couverture morte. Au moyen de simulations basées sur les données publiées, l'auteur discute de l'importance des exportations d'éléments lors de l'exploitation de la matière ligneuse, en fonction de la longueur de révolution, et des conséquences possibles de ces exportations de la productivité des stations.

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1. INTRODUCTION

Much interest has been raised in the last 10-15 years about intensively-cultured plantations harvested in short rotations as a means to help meet the increased demand for wood products, or as a source of energy. In particular, attention has been focused on poplars because they grow rapidly, are easily propagated, respond well to cultural treatments, and have been genetically-improved with potential for more improvement.

Populus is among the most ubiquitous of tree genera. The genus is composed of five sections, of which the most important (Leuce, Tacamahaca, and Algeiros) are largely spread in the Northern Hemisphere to which they are restricted. Much of the variation in their nutritional characteristics may relate to their inherent dissimilar growth rates.

High rates of tree productivity are associated with high rates of nutrient uptake and accumulation. Thus both growth and nutrients are important considerations in planning and managing plantations in order to optimize yield while maintaining or improving site productivity. This implies that biomass-nutrient relationships be considered in the broader context of nutrient cycling (Switzer and Nelson, 1973, Switzer *et al.*, 1978).

This review attempts to inventory and bring together published information dealing with all aspects of the nutrient cycle in *Populus*, irrespective of species or clone, or section, and of climatic conditions. Few studies encompass most aspects relating to the three cycling processes proposed by Switzer and Nelson (1972). Studies dealing with hybrid poplar nutrition in nurseries enable estimates of nutrient requirements of closely-spaced plantations of young poplars. Similarly, published work on litter production and chemical composition are important in assessing the range and magnitude of the biogeochemical cycle of nutrients in *Populus*. Specific aspects of amending poplar nutrition, such as fertilization, or aspects related to the use of nitrogen-fixing plants in poplar plantations, are not discussed in this review.

2. REVIEW OF NUTRITION AND NUTRIENT CYCLING

2.1 Productivity of Poplars

Productivity of forests and their rate of nutrient acquisition, retention and circulation are so intimately linked together that any discussion on nutrient cycling in stands or plantations has to highlight first the rate of growth and biomass accumulation of the species involved.

Mean annual increment of stems and branches. Reports from several sources show that hybrid poplars on good, adequately-prepared sites, reach mean annual increments of stems and branches (MAIsb) of 8-10 t ha⁻¹yr⁻¹ during the first 10 years in several countries in temperate and

Table 1. Selected mean annual increments of dry stems and branches reported for *Populus*

Species or clone	Location	Age (yr)	Trees ha ⁻¹	MAI ^{a,b} (t ha ⁻¹ yr ⁻¹)	Reference
<i>P. x euram.</i> 'I-476'	Italy 42°N	13	280	13.4	Rossi Marcelli <i>et al.</i> , 1980
<i>P. x euram.</i> 'I-214'	Italy 45°N	2 ^a	9100	11.0	Frison, 1968
<i>P. x euram.</i> 'I-214'	France 45°N	10	236-556	9.6	Barnéoud and Bonduelle, 1979
<i>P. x euram.</i> 'I-45/51'	Ontario 45°N	6 ^b	37000	9.3	Anderson, 1979
<i>P. deltoides</i>	Mississippi 32°N	12	1100	9.4	Switzer <i>et al.</i> , 1976
<i>P. x inter.</i> 'Rochester'	France 47°N	5	3000-9000	11.4-12.7	Bonduelle, 1979
<i>P. trichocarpa</i>	Washington 48°N	8	27000	9.4	Neilman and Peabody, 1981
<i>P. trich.</i> 'Fritz Paulay'	U.K. 52°-56°N	5	>5000	6-10	Cannell, 1980
<i>P. cv.</i> 'Tristis-1'	Wisconsin 45°N	5	6900	8.4	Isenhardt <i>et al.</i> , 1982

^a Two-year-old stem with three-year-old roots^b Three two-year coppices

Mediterranean regions (Table 1). Growth of *Populus* in its juvenile phase may be outstanding, and recent applications of agricultural methods to grow trees have shown that yields higher than those reported in Table 1 may be obtained.

Cannell and Smith (1980) reviewed published reports on yields obtained for plantations of *Populus* in 1-5 year rotations. They concluded that the "working maximum" MAIsb of 4- to 5-year-old minirotation plantations, in much of the temperate zone, seems to be $10-12 \text{ t ha}^{-1}\text{yr}^{-1}$, no greater than the MAIsb of some *Populus* plantations grown over 11-26 years. However, they indicated that 10-30% higher yields have been recorded at age 1-5 following coppicing.

Recent reports on plantations coppiced in short rotations indicate that exceptional yields, as high as $15-20 \text{ t ha}^{-1}\text{yr}^{-1}$, are not out of reach, provided plantations are established on rich alluvial soils (Bonduelle, 1979; Touzet, 1982) or are intensively cultured with fertilization, weed control and, occasionally, irrigation (Anderson, 1979; Hansen, 1980; Zavitskovski, 1981b; Zsuffa and Anderson, 1979). Clones most productive in widely-spaced plantations may be out-performed by more social clones with higher initial growth (Bonduelle, 1979).

The pattern of dry-matter accumulation in closely-spaced plantations obviously differs from that of widely-spaced plantations. Dense plantations reach maximum levels of MAIsb early, dependent on spacing, and then stabilize because competition reduces biological productivity per tree (Cannell, 1980; Hansen, 1980). However, there is evidence that after canopy closure plantation yield is independent of spacing (Cannell, 1980; Heilman and Peabody, 1981; Krinard and Johnson, 1980; Zavitskovski, 1981b) and is closely related to leaf area index (Hansen, 1980).

Net primary productivity. At least two published reports deal with net primary productivity (NPP) of poplar plantations; they are of considerable interest and enable comparisons with productivity of other systems.

For a plantation of *P. euram.* 'I-476' on alluvial soil in Italy, mean NPP reached $22.3 \text{ t ha}^{-1}\text{yr}^{-1}$ over 13 years, of which $20.5 \text{ t ha}^{-1}\text{yr}^{-1}$ was from overstory vegetation (Rossi Marcelli *et al.*, 1980). Production of stems and branches accounted for 66% of the NPP, or $13.4 \text{ t ha}^{-1}\text{yr}^{-1}$, the rest being allocated to litter and root production.

For *P. deltoides* plantations on alluvial soils of the lower Mississippi Valley, NPP of aboveground overstory vegetation averaged $12 \text{ t ha}^{-1}\text{yr}^{-1}$ at 16 years (Shelton *et al.*, 1982). Annual production maximized at 4-6 years at $17 \text{ t ha}^{-1}\text{yr}^{-1}$, close to the reported maximum for warm-temperate deciduous forests.

Litter production. Litter production in closed-canopy temperate deciduous forests may exceed $6-7 \text{ t ha}^{-1}\text{yr}^{-1}$ and, therefore, is a large part of the NPP (Bray and Gorham, 1964).

Although much information is available on litter production in natural stands of *Populus*, relatively few studies deal with plantations of hybrid

Table 2. Reported annual litter production in *Populus* stands and plantations

Species and clone	Age (yr)	Location	Aboveground litter production (kg ha ⁻¹ yr ⁻¹)			Reference
			Leaf	Overstory	Total	
<u>Natural stands</u>						
<i>P. tremuloides</i>	40	Minnesota 47°N			4289	Perala and Alban, 1982a
	49	"			3675	"
<i>P. tremuloides</i>	40	Utah 41°N	1610			Bartos and DeByle, 1981
<i>P. tremuloides</i>	10	Alaska 65°N	1100	1311		Van Cleve and Noonan, 1975
	50	"	1778	2187		"
	120	"	1623	2222		"
<i>P. tremuloides</i>	69	Alberta 50°N	2346	3176	1030	Cragg et al., 1977
<i>P. tremuloides</i> ^a		Alberta 51°N	2500	3160	990	Lousier and Parkinson, 1976
<i>P. tremula</i>	10	USSR 52°N	3851 ^b			Remezov and Bykova, 1953
	25	"	4100 ^b			"
	50	"	4880 ^b			"
<i>P. nigra</i>	35	Hungary 47°N			4000	Járo, 1958
<i>P. alba</i>	30	"			4600	"
<u>Plantations</u>						
<i>P. x euram.</i> 'I-214' (130x10-12) ^c	1	Italy 45°N	4496			Frisson, 1975a
<i>P. x euram.</i> 'I-214' (140x50)	1	Italy 42°N	2712			Giulimondi, 1970
	2	"	6151			"
<i>P. x euram.</i> 'I-476' (600x600)	10-13 ^d	Italy 42°N	5377	5929	1207	Rossi Marcelli et al., 1980
<i>P. cv.</i> 'Tristis-1' (30x30; 60x60)	3-7 ^b	Wisconsin 45°N	4000-			Zavitkovski, 1981a
			4200			

^a With some admixture of *P. balsamifera* and coniferous species^b Contains twig fragments^c Spacing (cm)^d Average for the ages mentioned

poplars (Table 2). Cumulative overstory litter production in a widely-spaced plantation of the euramerican hybrid 'I-476' reached 65.9 t ha^{-1} (97% leaves) over 13 years, or 22.7% of the aboveground net primary production (Rossi Marcelli *et al.*, 1980). Maximum rates of $7.2\text{--}7.5 \text{ t ha}^{-1}\text{yr}^{-1}$ were reached at age 5-7. The contribution of branches was initially negligible but accounted for 7-14% of the total overstory litter production by age 10-13. Litter production of $4\text{--}6 \text{ t ha}^{-1}\text{yr}^{-1}$ was also recorded in 1- to 4-year-old closely spaced plantations of hybrid poplars (Table 2).

This data suggests that $5.5\text{--}6.0 \text{ t ha}^{-1}\text{yr}^{-1}$ may be considered as an average litter production in highly productive hybrid poplar plantations grown in short or medium rotations and that leaf litter contributes 90% or more of the total overstory litter production before age 10. This is substantially higher than the production reported for natural stands of Leuce poplars (Table 2), and above the average $5.4 \text{ t ha}^{-1}\text{yr}^{-1}$ reported for established temperate deciduous forests (Cole and Rapp, 1981) or the average of $5.5 \text{ t ha}^{-1}\text{yr}^{-1}$ reported by Bray and Gorham (1964) for warm-temperate forests.

Studies on seasonal distribution of litter production in young plantations of *Populus* revealed that patterns of deposition vary with years and with spacings (Zavitkovski, 1981a). Litter production is little affected by stand density in closed-canopy stands (Sviridova, 1960). Leaf-fall initiation of hybrid poplars may start as early as July, and 25-40% of the total leaf-fall may occur before the period of maximum deposition in October or November; fallen leaves are replaced by newly-formed leaves resulting in an almost constant foliar mass (Frison, 1975a; Giulimondi, 1970; Giulimondi and Duranti, 1974; Zavitkovski, 1981a). By comparison, the pattern of litter production by Leuce poplars in cool-temperate regions is distinctly seasonal (Cragg *et al.*, 1977; Lousier and Parkinson, 1976; Witkamp and van der Drift, 1961). There may be substantial differences among species and clones, and perhaps from year to year, in dry-weight loss of leaves during senescence; reported losses vary from 19% (Viro, 1955) to about 50% (Baker and Blackmon, 1977).

Litter production of understory vegetation may contribute a substantial proportion of the total litter in *Populus* stands (Table 2; Cragg *et al.*, 1977; Lousier and Parkinson, 1976; Rossi Marcelli *et al.*, 1980). Its contribution to the annual biogeochemical cycle of nutrients within the system generally far exceeds its contribution to weight.

2.2 Site and Nutrient Requirements

Soil nutrient levels. Poplars are well known for their fast growth capacity; however, sustained high yields of biomass are essentially dependent upon large pools of nutrients available in the soil, adequate soil aeration and sustained water availability throughout the growing season (Baker and Broadfoot, 1976; Frison, 1973, 1975b; Garbaye, 1980; van den Burg, 1977, 1980; van den Burg and Schoenfeld, 1978). Most papers dealing with site requirements for growing Algeiros and Tacamañaca poplars

and their hybrids indicate that ideal conditions for growth are generally met on deep, medium-textured, alluvial soils subject to recurrent flooding (Baker and Broadfoot, 1976; Frison, 1975b; Frison *et al.*, 1982; Schoenfeld, 1975). Successful poplar cultivation further relies upon intensive site preparation (Anderson, 1979; Bar-néoud and Bonduelle, 1979; Hansen *et al.*, 1979). Clearly, site selection is probably the most critical decision to be made in poplar cultivation (Anderson, 1979; Baker and Broadfoot, 1976, Bonduelle, 1979; Raitanen, 1980) and this appears to be particularly true for short rotation, coppiced plantations.

From a nutrient standpoint, soil requirements of fast-growing *Populus* include not only sustained high levels of available N, P, and K but also a high base status. Indeed, near neutral pH is necessary for sustained high yield production of Aigeiros poplars because of their high requirement for Ca (Baker and Broadfoot, 1976; van den Burg and Schoenfeld, 1978). Euramerican hybrids generally grow well on deep, weakly calcareous, alluvial soils (van den Burg and Schoenfeld, 1978) but the presence of free carbonate in the rooting zone may be detrimental to nutrition and growth (Frison *et al.*, 1982; Garbaye, 1979, 1980). In particular, iron chlorosis frequently develops in sites with shallow, often compact, calcareous soils (Frison *et al.*, 1982).

Apart from their lower optimal pH range (KCl : 5.0-5.5), Tacamahaca poplars and their hybrids are considered to have much the same nutrient requirements as Aigeiros poplars (van den Burg, 1980; van den Burg and Schoenfeld, 1978). They are also adversely affected by the presence of free carbonate in the soil surface horizon (Garbaye, 1980; Garbaye and LeRoy, 1973; van den Burg and Schoenfeld, 1978).

Leuce poplars are more frugal and much less site-demanding in terms of moisture and soil base status than Aigeiros and Tacamahaca poplars (FAO, 1980). Yet their requirements for N and P per unit of production are comparable to that of poplars of other sections. Leuce poplars are adapted to a wide range of sites; their role in secondary successions may be similar to that reported by Marks (1974) for *Prunus pennsylvanica* in preventing disturbed sites from losing a significant part of the temporarily high nutrient capital made available after fire or harvesting (Adams, 1980).

Foliar nutrient levels. The relative nutrient requirements of the three main sections of *Populus* are reflected in the chemical composition of their foliage (Table 3). Mid- to late-summer concentrations of N and P in the foliage of field-grown trees may be much the same for a wide variety of *Populus* within the three sections, thus reflecting uniform N and P requirements of *Populus* in general. This seems to be supported by reports indicating similar optimum levels of 2.4-2.8% N in the foliage of euramerican hybrid poplars (Fritzsche, 1964; Garbaye, 1980; Schoenfeld, 1975; van der Meiden and Kolster, 1964) and of Leuce poplars (Mitchell and Chandler, 1939; Viro, 1955). Similarly, the same critical N concentration of 2.0% is reported for the foliage of *P. deltoides* (Blackmon, 1976, 1977a; White and Carter, 1968; Shelton *et al.*, 1981) and *P. tremuloides* (Mitchell and Chandler, 1939). The greatest difference in foliar nutrient concentrations between the three main sections of *Populus* probably lies in

Table 3. Range of reported average foliar nutrient concentrations of *Populus* in mid- to late-summer (and reported critical levels for *P. deltoides*)

Section	Age (yr)	Percent of oven-dry weight					Reference
		N	P	K	Ca	Hg	
Algeiros							
Hybrids ^a	1-19	2.1- 2.8	0.19- 0.26	1.5- 2.0	1.9- 2.6	0.30- 0.35	7,8,9,10,11,19
		2.0	0.17	1.3	2.2	0.18	4,5,17
Critical levels ^{ab} (<i>P. deltoides</i>)							
Algeiros-Tacamahaca							
Hybrids ^c	1-2	2.0- 2.2	0.24- 0.26	1.5- 1.7	1.4- 1.6	0.20- 0.27	10
	3-20	2.1- 2.6	0.20- 0.23	0.9- 1.2	1.1- 1.7	0.22- 0.30	15,16
Tacamahaca ^d							
	12-60	2.1- 2.6	0.17- 0.26	0.8- 1.5	1.0- 1.6	0.11- 0.25	1,2,3,6,12,13,14,18,20,21
Leuca ^e							

^a Clones: Gelrica, I-214, I-45/51, I-476, Régénéf, Robusta, Yardif, Virginie

^b Weighted mean for all crown positions

^c Clones: Androscoggin, Fritzi-Pauley, Oxford, Rochester

^d *P. canadensis*, *P. trichocarpa* x *P. maritima* var. *lasi* (Ca excluded)

^e *P. tremula*, *P. tremuloides*, *P. grandidentata*

1. Alban et al., 1978

2. Bard, 1946

3. Bartos and Johnson, 1978

4. Blackton, 1977a

5. Carter and White, 1970

6. Ducet and Veilleux, 1982

7. Frison, 1969a

8. Frison, 1979

9. Garbaye, 1980

10. Garbaye and Leroy, 1973

11. Giullimondi and Duranti, 1974

12. James and Smith, 1977

13. Mitchell and Chandler, 1939

14. Rodin and Basilevich, 1967

15. Sheedy and Vallée, 1976

16. Sheedy and Vallée, 1981

17. Shelton et al., 1981

18. Tew, 1970

19. Touzet and Heinrich, 1970

20. Verry and Timmons, 1976

21. Viro, 1955

the base elements, particularly Ca which ranks in the order : Aigeiros > Tacamahaca > Leuce (Table 3). This difference stresses the higher soil base status requirements of Aigeiros poplars (Baker and Broadfoot, 1976; Garbaye, 1980). Critical levels of foliar Ca for *P. deltoides* (Blackmon, 1977a; Shelton *et al.*, 1981; White and Carter, 1968) are 1.5 to 2.0 times higher than Ca concentrations commonly reported in the foliage of Leuce poplars (Table 3).

Caution must be exercised in interpreting foliar analysis since there are considerable variations in the reports over a wide range of growing conditions. Much of this variation is due to season, crown position, climate, soil composition, provenance and clonal differences (Baker and Randall, 1975; Blackmon *et al.*, 1979; Broadfoot and Farmer, 1969; Frison, 1979; Garbaye, 1972; Nakos, 1975; Touzet and Heinrich, 1970). Age and density of the plantation have little, if any, effect on foliar nutrient concentrations (Ogar, 1981; Shelton *et al.*, 1981). Concentrations of N, P and K much above those in Table 3 are commonly reported for greenhouse-grown (Leech and Kim, 1981) or plantation-grown hybrid poplars intensively cultured to maximize growth (Ek and Dawson, 1976; Hansen, 1976).

Nutrient requirements. The nutrient requirements of hybrid poplars in the nursery illustrate the high initial nutrient requirements of closely-spaced hybrid poplar plantations (Table 4). Such high requirements are comparable to those of several agricultural crops (Frison, 1969a) and may be more than twice the requirements of conventional plantations of *P. deltoides* (Shelton *et al.*, 1982) or established temperate deciduous forests, and several times that of established temperate coniferous forests (Table 5). The difference is most striking for Ca and reflects both the inherent higher growth rate of the hybrid poplars and their higher nutrient requirements per unit biomass production. On that basis, an average 13 kg N, 1.5 kg P, 8 kg K, 10 kg Ca and 2 kg Mg would be required for the production of one ton of aboveground biomass of poplar, aside from the demands for roots (Table 4). Foliage accounts for about two thirds of the annual nutrient needs. Requirements per unit dry matter produced are not influenced by mode of culture (Switzer *et al.*, 1976).

The pattern of change in the nutrient requirements with age in widely-spaced plantations is well documented (Miller, 1981; Ovington, 1959; Switzer and Nelson, 1972). The demand is greatest in the early formative stage of stand development when the canopy, roots and stem are developing (Attiwill, 1979; Switzer *et al.*, 1978). For *P. deltoides* plantations on alluvial soils in the lower Mississippi Valley, Shelton *et al.* (1982) estimated that annual requirements were maximum from age 4-6 years at about 100, 12, 20, 150 and 18 kg ha⁻¹yr⁻¹ for N, P, K, Ca and Mg, respectively. Requirements are expected to remain at these levels since after crown closure the greatest share of the stand's nutrient requirements is used in the formation of foliage which has a fixed rate of replacement. Therefore, the initially low nutrient requirement : nutrient accumulation ratio widens with stand age, not so much because of change in the requirement rate as for a decrease in the nutrient accumulation rate which reflects a decreasing contribution of the crown to total weight and the development of internal cycling.

Table 4. Reported annual nutrient requirements of *Algeiros* poplars in nursery (aboveground components only)

Species and clone (spacing, cm)	Year	Biomass production (t ha ⁻¹ yr ⁻¹)	Nutrient (kg ha ⁻¹ yr ⁻¹)				Reference
			N	P	K	Ca	
<i>P. x europ.</i> , 'I-214' (120x7-8)	1	14.5	198	23.2	123	149	Frison, 1969a
<i>P. x europ.</i> , 'I-45/51' (120x7-8)	1	12.0	182	19.8	113	121	Frison, 1969a
<i>P. x europ.</i> , 'I-214' (120x7-8)	1 ^a	22.2	238	35.2	167	229	Frison, 1969a
<i>P. x europ.</i> , 'I-45/51' (120x7-8)	1 ^a	20.9	244	35.8	171	212	Frison, 1969a
<i>P. x europ.</i> , 'I-214' (150x50)	2	24.4	246	27.3	158	237	Giulimondi and Duranti, 1974

^a One-year-old stem with two-year-old roots

Table 5. Annual nutrient requirements of *Algeiros* poplars in nursery or in plantation compared to requirements of established forests of other tree genera (aboveground, overstory)

Vegetation (location)	Age (yr)	Aboveground production (t ha ⁻¹ yr ⁻¹)	Requirement (kg ha ⁻¹ yr ⁻¹)				Reference
			N	P	K	Ca Mg	
<i>P. x euramericana</i> (Italy)	1-2	12-24	182- 246	20- 36	113- 171	121- 237	38 See Table 4
<i>P. deltoides</i> (Mississippi, U.S.A.)	4-6	17	102	11.5	88	151	17.9 Shelton <i>et al.</i> , 1982
<i>Betula</i> (Finland)	40	6.9	78	6.5	33	39	Mäkilinen, 1977
<i>Fagus</i> (Germany)	80	9.6	107	6.7	38	28	3.4 From Cole and Rapp, 1981a
<i>Acer-Betula-Fagus</i> (New Hampshire, U.S.A.)	60	7.9	90	7.4	38	38	6.6 From Cole and Rapp, 1981a
Temperate deciduous (ave. 14 sites) ^b	30-120	10.0	98	7.2	48	56	10.4 Cole and Rapp, 1981
Temperate coniferous (ave. 13 sites) ^b	15-450	8.3	46	5.5	28	20	4.6 Cole and Rapp, 1981

^a Values quoted by Cole and Rapp from work of Ulrich, Ellenberg; Whittaker, Likens
^b Europe and North America

Few studies have investigated the requirements for roots. For one-year-old *P. deltoides* in plantation, Baker and Blackmon (1977) reported root contributions of 34% of total tree biomass and 32, 47, 42, 25 and 17% of total tree accumulation of N, P, K, Ca and Mg, respectively, before initiation of leaf senescence.

2.3 Nutrient Accumulation

Accumulation in biomass. Because of their inherent high rate of growth and the relatively high nutrient concentration in their crown tissues, poplars accumulate nutrients more rapidly in stands or plantations than most temperate forests (Table 6). Although such comparisons are confounded by differences in age among forests, it indicates contrasting rates of accumulation among nutrients in different forest types. For instance, Ca accumulation is twice as high as N accumulation in *Populus*, a much higher ratio than that of most other forests. Foliage accounts for less than 3-7% of the accumulated dry weights of forests listed in Table 6, but its contribution to nutrient accumulation is much higher, particularly in younger stands. Thus, more practical attention is given here to nutrient accumulation in perennial components - stem and branches.

Accumulation in stem and branches. Hansen and Baker (1979) reviewed the influence of tree age, cutting cycle, spacing and clone on rates of N accumulation in intensively-cultured plantations. They concluded that N utilization efficiency (kg of dry matter/kg of N) increases markedly with age, because of dilution brought about by relative increases in woody biomass. It reaches an almost stable value beyond 7-8 years, close to that of natural stands.

Reports by Frison (1967, 1968, 1969a) and Giulimondi (1970) on the accumulation of nutrients in nursery stock of euramerican hybrid poplars show that initial mean annual rate of nutrient accumulation in stems and branches is 4- to 6-times the mean annual accumulation rate of 16-20 kg N, 4-6 kg P and 20-25 kg K per hectare of adult plantations (Frison, 1969b, 1978; Giulimondi, 1966a). Yet, these latter rates are 1.5- to 2-times greater than those reported for 20-year-old stands of *P. deltoides* (Switzer *et al.*, 1976) and almost 3 times those of adult stands of *P. tremuloides* (Alban *et al.*, 1978; Perala and Alban, 1982a). Obviously, rate of nutrient accumulation decreases with age but these differences also reflect differences in inherent growth rates among species and clones.

The dry weight and nutrient contents of unfertilized (or initially weakly fertilized) plantations and unfertilized natural stands of *Populus* appear in Table 7. When nutrient accumulation is plotted against dry-weight accumulation (Figure 1), distinct patterns emerge showing markedly higher accumulations associated with lower dry-weights ($<30 \text{ t ha}^{-1}$), suggesting an age-related relationship, except for Ca accumulation which closely follows dry-weight accumulation.

Before age 8-10, with the exception of Ca, age is probably the most determining factor of gross nutrient concentration (Figure 2). Because data originate from several different sources and include many species and clones, this further suggests that accumulation of nutrients per unit weight of

Table 6. Aboveground overstory biomass and nutrients in selected *Populus* stands compared to the amounts reported for forests of other tree genera

Species or genus (location)	Age (yr)	Aboveground biomass (t ha ⁻¹)	Nutrient (kg ha ⁻¹)				Reference
			N	P	K	Ca	
<i>P. tremuloides</i> (Minnesota, U.S.A.)	40	166.8	368	46	287	858	Alban et al., 1978
<i>P. deltoides</i> (Mississippi, U.S.A.)	20	141.0	351	56	332	737	Switzer et al., 1976
<i>P. x euram.</i> 'I-214' (Italy)	10-13 ^a	96.4	278	45	290	633	Frison, 1978
<i>Betula</i> (Finland)	40	90.2	214	21	112	176	Mäkiläinen, 1977
<i>Quercus-Carya</i> (Tennessee, U.S.A.)	30-80	121.6	369	24	220	856	From Cole and Rapp, 1981 ^b
<i>Acer-Betula-Fagus</i> (New Hampshire, U.S.A.)	60	134.0	367	33	154	402	From Cole and Rapp, 1981 ^b
<i>Fagus</i> (Germany)	59	154.6	407	26	130	324	From Cole and Rapp, 1981 ^b
Temperate deciduous (ave. 14 sites) ^c	30-120	151.9	442	35	224	557	Cole and Rapp, 1981
Temperate coniferous (ave. 13 sites) ^c	15-450	307.3	479	68	340	480	Cole and Rapp, 1981

^a Normal rotation period in Italy. Current foliar nutrient stocks assumed for 6.4 t of foliage (Frison, 1969b)

^b Values quoted by Cole and Rapp from work of Harris, Henderson; Whittaker, Likens; Ulrich, Ellenberg

^c Europe and North America

Table 7. Reported dry weights of stem and branches and their nutrient contents in *Populus* stands and plantations

Species or clone (spacing, cm)	Age (yr)	Dry weight (t ha ⁻¹)	Nutrient (kg ha ⁻¹)				Reference
			N	P	K	Ca	
<i>P. deltoides</i> (300x300)	20 ^a	90.2	167	31	175	384	42 Switzer et al., 1976
<i>P. deltoides</i> (natural)	20	135.4	258	46	271	579	64 Switzer et al., 1976
<i>P. deltoides</i> (300x300)	16	65.3	100	17.1	127	299	31 Shelton et al., 1982
<i>P. deltoides</i> (300x300)	1 2	1.5 7.8	14 50	1.5 7	7 25	9 45	1.6 7 Baker and Blackmon, 1977 Baker and Blackmon: In Hansen and Baker, 1979
	3 4	15.0 26.9	62 101	11 18	52 92	120 203	16 25 "
<i>P. deltoides</i> (300x300)	7	77.7	157	23.5	155	418	34 Carter and White, 1970; White, 1974
	8	75.1	138	26.9	160	328	32
<i>P. deltoides</i> (natural)	7 ^b 8 ^b	62.2 65.6	135 158	24.1 17.3	148 128	305 287	31 32 "
	9	63.7	146	15.7	127	308	36 "
<i>P. x euram.</i> (120x7-8)	1 ^c 2 ^{cd}	10.0 26.2	86 148	12.4 23.4	44 93	58 140	Frison, 1967, 1969a "
<i>P. x euram.</i> (170x65)	2 ^{cd}	23.6	133	21.1	83	126	Frison, 1968
<i>P. x euram.</i> (140x50)	2	42.7	203	29.3	116	237	Giulimondi, 1970

(continued on next page)

Table 7 (continued)

Species or clone (spacing, cm)	Age (yr)	Dry weight (t ha ⁻¹)	Nutrient (kg ha ⁻¹)				Reference
			N	P	K	Ca	
<i>P. x euram.</i> 'I-214' (750x550)	10	115.3	197	56.3	254	458	Giulimondi, 1966a
<i>P. x euram.</i> 'I-214' (150x50)	2	19.7	120	17.1	52	115	Giulimondi and Duranti, 1974
<i>P. x euram.</i> 'I-214' (130x10-12)	1	10.6	93	13.6	47	-	Frison, 1975a
<i>P. x euram.</i> 'I-214'	11 ^e	90.0	163	32.8	199	414	Frison, 1973, 1975b, 1978
<i>P. x euram.</i> 'I-214' (60x20)	1	18.2	179	19.8	91	113	Dzekova, 1972
<i>P. x euram.</i> 'I-45/51' (120x7-8)	1 ^d 2 ^d	7.5 25.1	68 178	9.9 26.6	35 92	36 121	Frison, 1967, 1969a
<i>P. x euram.</i> 'I-45/51' (170x65)	2	22.6	133	24.0	82	109	Frison, 1968
<i>P. x euram.</i> 'I-45/51' (30x30 -- 300x300)	2 ^f	3.6	32	3.2	9	18	Ogar, 1981
<i>P. x euram.</i> 'I-45/51' (60x20)	18	18.3	179	27.8	103	115	Dzekova, 1972
<i>P. x euram.</i> 'Robusta' (30x30 -- 300x300)	2 ^f	3.4	24	2.5	8	20	Ogar, 1981
<i>P. x euram.</i> 'Robusta' (60x20)	1	12.6	120	17.6	60	79	Dzekova, 1972

(continued on next page)

Table 7 (continued)

Species or clone (spec., cm)	Age (yr)	Dry weight (t ha ⁻¹)	Nutrient (kg ha ⁻¹)				Reference
			N	P	K	Ca	
<i>P. x euram.</i> 'I-455' (60x20)	1	15.0	142	17.7	82	94	Dzekova, 1972
<i>P. tremuloides</i> (natural)	40	163.2	281	37.5	240	821	Alban et al., 1978; Perala and Alban, 1982a
<i>P. tremuloides</i> (natural)	49	148.8	265	38.1	184	861	Perala and Alban, 1982a
<i>P. grandidentata</i> (natural)	12 ^b	8.1	15	2.9	15	32	Schmidt et al., 1981

^a Thinned plantation^b Average of two stands^c Soil normally treated before planting with 30 t ha⁻¹ manure, 500 kg ha⁻¹ phosphate (18-20% P₂O₅), 150 kg ha⁻¹ potash (40-42% K₂O), 70 kg ha⁻¹ urea (46% N)^d Two-year-old stem with three-year-old roots^e 10-13 year rotation^f Average of ten spacings, control (unfertilized) plots^g Nutrient contents reported by Dzekova include roots within the total-tree samples from plants lifted after complete leaf fall to evaluate nutrient removal from nursery. The above-reported data of nutrients in stem and branches result from apportioning nutrient contents to measured weight (air-dry basis) of stem and branches assuming uniform concentrations of elements in the whole plant^h Contribution of bigtooth aspen only

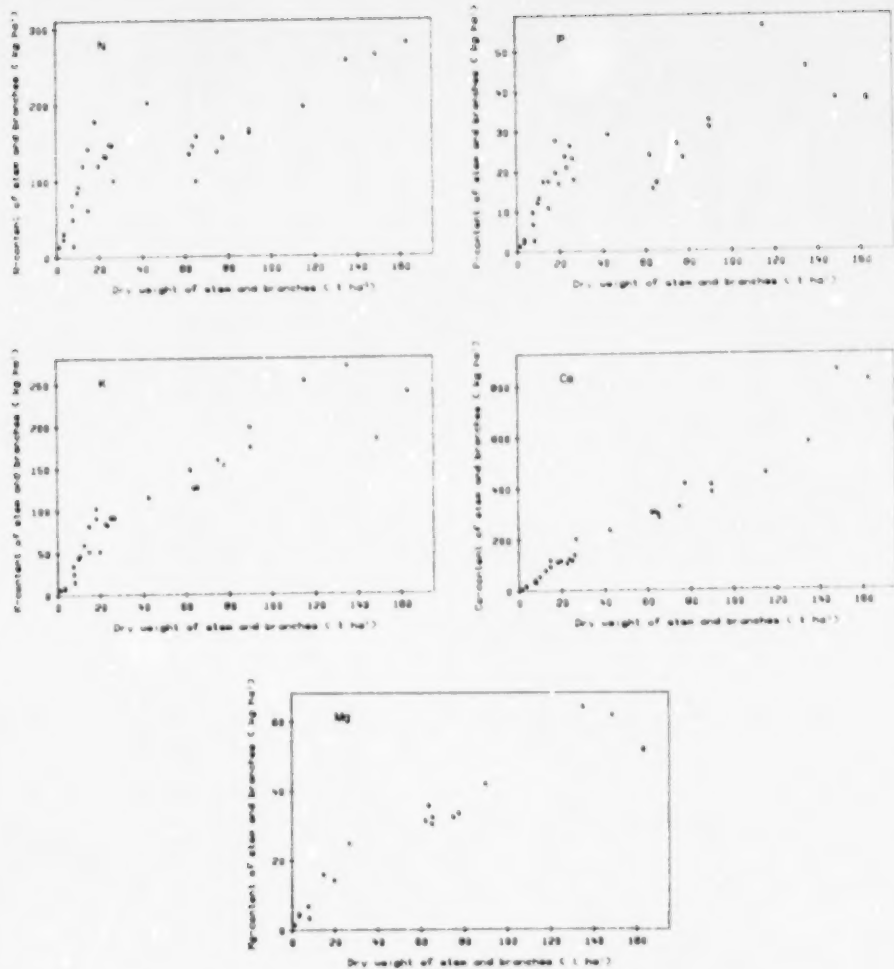


Figure 1. The relationships of nutrient content of stem and branches to accumulated dry weights of stem and branches in *Populus* (data from Table 7).

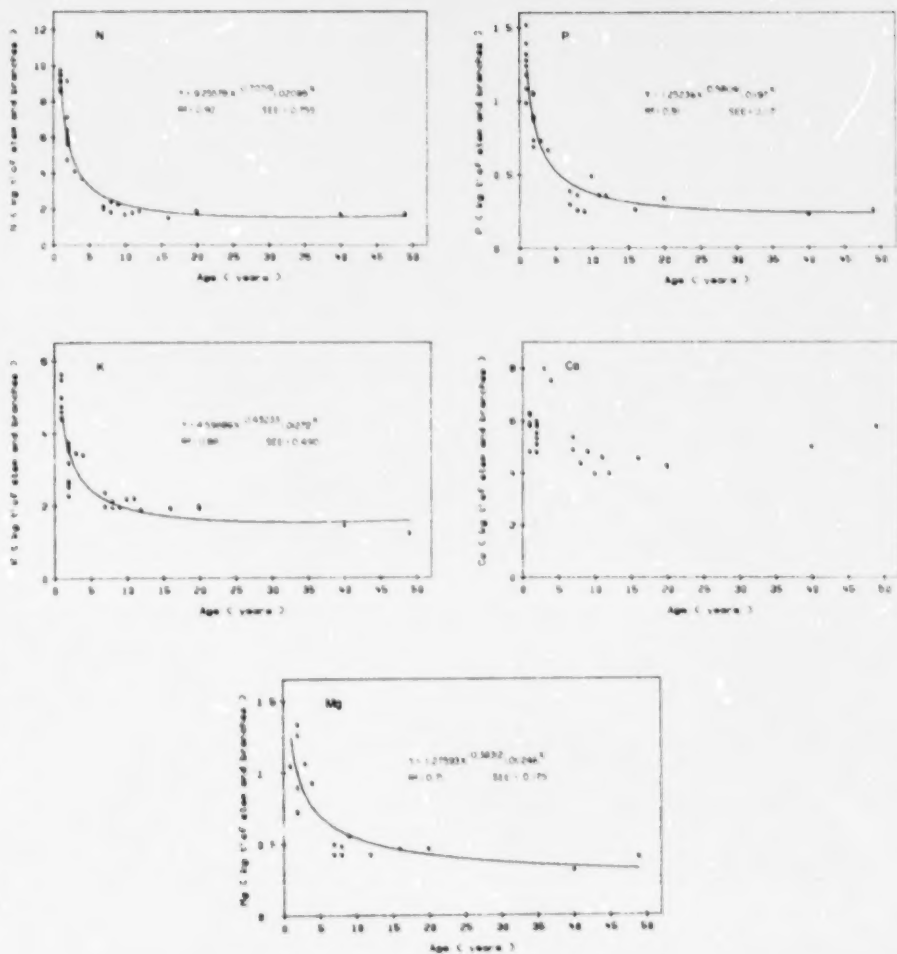


Figure 2. Gross concentration of nutrients (kg t⁻¹) in stem and branches of *Populus* as a function of age (data from Table 7).

stem and branches, at a given age, is relatively independent of species and of production level, a conclusion already arrived at by Hansen and Baker (1979) for N. This implies that most *Populus* growing in these conditions contain, at age 1, approximately 8-10 kg N t⁻¹, 1.0-1.5 kg P t⁻¹, 4.5-5.5 kg K t⁻¹, 4-6 kg Ca t⁻¹ and 1.3 kg Mg t⁻¹. Except for Ca, which remains apparently unchanged, gross nutrient concentrations progressively decrease with age to approximately 1.8-2.0 kg N t⁻¹, 0.3-0.4 kg P t⁻¹, 1.2-2.2 kg K t⁻¹, and 0.4-0.5 kg Mg t⁻¹ by age 8-10, and subsequently remain almost constant. Gross nutrient concentrations at a given age appear to be independent of yield, a conclusion supported by a spacing x nutrient-accumulation study with 2-year-old euramerican hybrid poplars (Ogar, 1981).

Regression equations predicting gross nutrient concentrations from stand age were calculated and they fit the data well, except for Ca (Figure 2). Because several factors other than age, including provenance (Blackmon *et al.*, 1979), season (Baker and Blackmon, 1977; Frison, 1975a; Giulimondi and Duranti, 1974) and luxury consumption (Chapin, 1980; Turner, 1977) influence nutrient concentration in stem and branches, caution should be exercised in using these regressions as prediction models for nutrient accumulation. Luxury supply of nutrients, induced by heavy or repeated fertilizer applications, is perhaps the most common cause of increased nutrient concentrations in woody tissues.

2.4 Sources of Nutrients and Nutrient Cycling Processes

Nutrient storage, translocation and seasonal changes. Changes in the concentration of elements in foliage and other tissues involve several processes including dilution, storage, translocation and leaching.

Seasonal changes in foliar nutrient concentrations were studied for several species and clones of *Populus*, including *P. tremula* (Smirnov and Semenova, 1972), *P. tremuloides* (Tew, 1970; Verry and Timmons, 1976), *P. deltoides* (Baker and Blackmon, 1977), *P. x euram.* 'I-214' (Frison, 1975a, 1979; Garbaye, 1972; Giulimondi, 1966b; Giulimondi and Duranti, 1974; Touzet and Heinrich, 1970), *P. x euram.* 'I 45/51' (Nakos, 1975; Ogar, 1981) and *P. x euram.* 'Robusta' (Garbaye, 1972; Nakos, 1975; Ogar, 1981; van der Meiden and Kolster, 1964). As a rule, Ca and Mg concentrations increase over time, while N, P and K concentrations peak early in the season. The seasonal increase of Ca and Mg results from dry weight losses during senescence while the decline of N, P and K is due initially to dilution by increasing leaf biomass and later to translocation out of the leaves (Chapin, 1980). Few studies, however, covered the entire autumnal senescence.

Translocation of nutrients from foliage to other plant parts before abscission is probably the most important contributing source to the internal storage pool from which deciduous species draw upon for initiation of their annual growth. In *Populus*, as in most deciduous species (Chapin, 1980; Chapin *et al.*, 1980; Ryan and Bormann, 1982), N and P are the nutrients most involved. According to Cole (1981), about one third of N and P requirements of temperate deciduous forests is accounted for by translocation.

Studies of nutrient uptake and dry-weight accumulation by the euramerican hybrid 'I-214' provided evidence of important seasonal transfer and storage of nutrients (Frison, 1975a; Giulimondi and Duranti, 1974). The early peak rate of N, P and K accumulation in foliage was accompanied by decreasing pool sizes of these nutrients in stem and branches, suggesting that foliar growth was initially supported by stored nutrients (Giulimondi and Duranti, 1974). These studies revealed that more of the foliar N was externally cycled than was translocated and stored internally. In support of this is the high N concentration in freshly fallen leaf litter of euramerican hybrids under Mediterranean climates in these and other studies (Duranti and Giulimondi, 1980; Giulimondi, 1970). While N is stored mostly in bark, more than half of P storage may be in the wood (Frison, 1975a).

For one-year-old *P. deltooides* grown in plantation, Baker and Blackmon (1977) estimated that 61% of the N and 53% of the P contained in the foliage were withdrawn before leaf abscission and stored in branch bark, stem bark and roots. Of particular interest in their study is the late season gain of N (46%) and P (14%) in roots. The quantity of N and P translocated from leaves was 47% of the total N and 32% of the total P used in aboveground production.

Amounts of nutrients involved in internal transfer and storage are expected to increase with the increase of foliage production and to reach stable quantities, and maximum contribution to requirements, only after crown closure (Miller, 1981). Shelton *et al.* (1982) estimated that of the 1128 kg N ha⁻¹ and 124 kg P ha⁻¹ used in net primary production over 16 years in thinned plantations of *P. deltooides*, 41% of the N and 30% of the P were involved in this transfer.

None of the above-mentioned studies report any significant translocation of K, Ca and Mg because their loss from leaves was not accompanied by accumulation in perennial tissues. Rather, in the euramerican hybrid 'I-214', K was lost not only from leaves (Giulimondi and Duranti, 1974) but from wood and bark as well (Frison, 1975a; Giulimondi and Duranti, 1974). Extensive loss of K from foliage was attributed to leaching or exudation (Baker and Blackmon, 1977; Giulimondi and Duranti, 1974) while loss from wood and bark apparently involved leaching and root exudation or sloughing (Frison, 1975a). Despite a decrease in K content of wood and bark, both tissues still contained about half of their maximum pool sizes in December (Frison, 1975a), thus suggesting that storage of K in these tissues may be significant. The 34% net deficit of K measured from roots of *P. deltooides* in autumn (Baker and Blackmon, 1977) seems to support an extensive return of this element to the soil.

Evidence of seasonal nutrient transfers and storage was also provided by Vallée and Chamberland (1978) for clones of Aigeiros and Tacamahaca poplars, involving mostly N and little P. However, only part of the senescence period was apparently covered.

Translocation from senescing foliage also seems to be strongly developed in Leuce poplars of cool-temperate and boreal forests. For instance, Viro (1955) estimated that the net loss of elements from senesced foliage of *P. tremula* amounted to 78% of the N and 67% of the P (Table 8). Assuming

Table 8. Reported changes in foliar nutrient contents of *Populus* before abscission

Species	Age (yr)	Percent reduction of nutrients					Reference
		N	P	K	Ca	Mg	
<i>P. tremula</i> ^a	30-60	78	67	58	23	-14 ^b	Viro, 1955
<i>P. deltoides</i>	1	74	67	72	38	49	Baker and Blackmon, 1977

^a Yellow leaves collected on trees during autumnal leaf-fall, not strictly litterfall

^b The negative sign indicates net increase

that leaching of N and P was small (Verry and Timmons, 1977), then the extent of their translocation from leaves to nonphotosynthetic tissues was of the same magnitude as that reported for *P. deltoides* (Baker and Blackmon, 1977). Several reports show that foliage of *P. tremuloides* undergoes decreases of N and P concentrations before abscission (Bartos and DeByle, 1981; Chandler, 1941; Cragg *et al.*, 1977; Deaubemire, 1953; Verry and Timmons, 1976). On the assumption that reduction in foliage weight is of the same magnitude as that measured in *P. tremula* (Viro, 1955), then about two-thirds of the foliar stocks of N and P would be involved in translocation and storage.

Translocation from aging wood and bark. Translocation of nutrients from senescing parenchymal cells of wood and bark appears to be an integral part of the biochemical cycling of nutrients (Attiwill, 1979, 1980; Bamber, 1976; Cowling and Merrill, 1966; Lambert, 1981). Indirect evidence of this process results from radial and longitudinal concentration gradients in wood and bark. Of particular importance in *Populus* is the decreasing concentration of P from outer to inner xylem, with the sharpest gradient (almost an order of magnitude) occurring at the sapwood - heartwood boundary (Clément and Janin, 1973, 1976; Janin and Clément, 1972). The process also involves N, but apparently to a lesser extent than P (Cowling and Merrill, 1966; Giulimondi, 1966a; Merrill and Cowling, 1966). Heartwood formation may not be initiated in *Populus* before age 7 or 8 (Clément and Janin, 1973; Janin and Clément, 1972), a time span about the same as that reported for eucalyptus (Crane, 1978; Crane *et al.*, 1981) but shorter than for most temperate deciduous species (Kramer and Kozlowski, 1979).

Changes in concentration of nutrients in bark of *Populus* through time (Frison, 1969b; Hansen and Baker, 1979; Shelton *et al.*, 1981) indicate that translocation of mobile nutrients occurs in aging phloem as in aging xylem. This process avoids the immobilization of significant amounts of nutrients, and enable their re-use in a way apparently similar to that resulting from

foliage senescence (Bamber, 1976; Wardell and Hart, 1973). In both processes, the levels of elements such as Ca and S either show little change or increase in concentration (Wardell and Hart, 1973).

Little is known about the contribution of aging wood and bark to the internal mobile pool of nutrients in *Populus*. In eucalyptus, it has been shown to account for about 40% of the biochemical cycle of P (Attiwill, 1981) and about 10% of the biochemical cycle of N (Baker and Attiwill, 1981; Turner and Lambert, 1981). Reports for other species include contributions of 28% and 31% of the biochemically-cycled N and P, respectively, in Douglas-fir (Turner, 1977) and 31% of the biochemically-cycled P in Corsian pine (Ranger, 1981).

Nutrient return in throughfall and stemflow. The extent of nutrient return by crown wash and stemflow in *Populus* systems has not been widely studied; however several papers point out their importance especially during autumn senescences (Frison, 1975a; Garbaye, 1972; Giulimondi and Duranti, 1974; Viro, 1955).

For a *P. tremuloides* stand in Minnesota, Verry and Timmons (1977) reported a net decrease of total N in throughfall and stemflow over incident precipitation, but increases of 3, 15, 4.5, and 5 times for P, K, Ca, and Mg, respectively. The order of leachability ($K > Mg > Ca > P > N$) is that most frequently reported. Despite its comparatively low quantity (< 10%), stemflow contributed 41, 44, and 37% of the aqueous transfers of K, Ca, and Mg, respectively. These contributions are much above the usual range of stemflow contribution in deciduous species (Cole and Rapp, 1981; Forgeard *et al.*, 1980; Reiners, 1972), and may reflect the high concentrations of these elements, particularly Ca, in aspen bark (Alban *et al.*, 1978; Bartos and Johnaton, 1978). Mahendrappa (1974) observed that *P. grandidentata* had the highest stemflow of Ca of the nine eastern North American species he investigated.

Some of the loss of foliar nutrients during senescence (Table 8) is due to leaching. While presumably less than 15% of the N and P losses may result from leaching (Baker and Blackmon, 1977), much of the K, Ca, and Mg is transferred to soil by this process (Baker and Blackmon, 1977; Frison, 1975a; Giulimondi and Duranti, 1974). Based on Baker and Blackmon's (1977) study, about one-third of the foliar Ca, one half of the foliar Mg and two-thirds of the foliar K would potentially be returned to the soil in aqueous transfers from canopy during leaf senescence. Throughfall returns are not limited to the leaf senescence period, but it is generally agreed that maximum transfer rates take place during that period (Chapin, 1980; Tukey, 1970).

The proportions of foliar stocks of nutrients involved in throughfall return are similar to those reported for several other species (Attiwill, 1980; Britson *et al.*, 1980; Eaton *et al.*, 1973; Gosz *et al.*, 1975; Henderson *et al.*, 1977; Ostman and Weaver, 1982). However, given the same climatic conditions, the amounts involved may be higher in *Populus* because of their generally higher foliar stocks of nutrients.

Nutrient return in litterfall. Reported rates of nutrient return associated with annual aboveground litterfall in various *Populus* systems (Table 9) show that the contribution of elements to litterfall is consistently in the order : $Ca > N > K > Mg > P$. There seems to be a good concordance between rates of nutrient return and rates of litter deposition (Figure 3); however, relationships are not linear within the genus because litter of Aigeiros poplars has higher concentrations of nutrients, except for P, than that of Leuce poplars (Table 10).

As might be expected, the highest reported rates of nutrient return were for plantations of fast-growing euramerican hybrid poplars under a Mediterranean climate (Table 9). These rates are 1.8- to 3.7-times higher than the average of temperate deciduous forests investigated by the IBP (Cole and Rapp, 1981). Peak rate of return in a widely-spaced plantation of *P. x euram.* 'I-476' reached a total of 554 kg ha⁻¹ of major nutrients at age 7, with Ca and N accounting for about 75% of the total nutrient return (Duranti and Giulimondi, 1980). In this case, the contribution of branches to overstory litterfall at age 10-13 was 9% for dry-weight but 2% for N, 3% for K and Mg, 5% for Ca, and 29% for P, thus stressing the proportionally high contribution of branch litter to the biogeochemical transfer of P.

The consistently higher return of Ca among nutrient elements in leaf litter reflects both high foliar stocks of Ca and retention during senescence. Calcium concentration in leaf litter is 2-3% of litter dry-weight. Similarly, the consistently lower return of P reflects both low foliar stocks of P and high translocation from senescing leaves. Therefore, the amount of P cycled through the litterfall pathway in *Populus* is, as for N, only a small proportion of the system's requirement for this element; however, in absolute amounts, the return may be high in comparison to that of temperate deciduous forests (Table 9).

Leaf litter of Aigeiros poplars has significantly higher nutrient concentrations than that of Leuce poplars, except for P (Table 10). The two-fold difference in N concentration is striking and results in the considerably higher biogeochemical transfer of N in Aigeiros poplars, at least under Mediterranean conditions. Conversely, less P is in circulation per unit leaf-litter weight which may reflect greater conservation within the trees. However, the high contribution of branch litter to the return of P (Duranti and Giulimondi, 1980) may progressively offset this difference.

As observed in other systems (e.g. Foster and Morrison, 1976; Mälkönen, 1977), the contribution of understory vegetation to total aboveground litter nutrient input in *Populus* systems may be proportionally higher than its contribution to litterfall mass, since nutrient concentrations are generally higher for understory litter. Thus, understory vegetation plays an important role in the overall cycling of nutrients. Although the relative contribution of elements to the total understory input varies with the system's characteristics, that of N, P and K are consistently the most important while that of Ca is the least important. Thus, for a 40-year-old *P. tremuloides* stand in Minnesota, understory vegetation contributed 19% of the total aboveground litter production and 36, 40, 59, 18 and 28% of the total litter N, P, K, Ca and Mg, respectively (Perala and Alban, 1982a).

Table 9. Reported annual return of nutrients in aboveground litterfall in *Populus* stands and plantations compared to litterfall nutrient return in IRP sites of temperate deciduous forests

Vegetation	Stand age (yr)	Location	Litter dry weight (kg ha ⁻¹ yr ⁻¹)	Nutrient (kg ha ⁻¹ yr ⁻¹)					Reference
				N	P	K	Ca	Mg	
<i>P. tremuloides</i>	40	Minnesota 47°N	(t) ^a 4289	38	8.0	22	80	8.5	Perala and Alban, 1982a
	49	"	(t) 3675	33	6.7	19	60	8.0	"
<i>P. tremuloides</i>	40	Utah 41°N	(l) 1610	8	0.9	7	30	1.8	Bartos and DeByle, 1981
<i>P. tremuloides</i>	10	Alaska 65°N	(o) 1311	11	2.1	5	28	3.8	Van Cleve and Noonan, 1975
	50	"	(o) 2187	22	4.8	10	48	6.8	"
	120	"	(o) 2222	19	3.4	6	40	6.2	"
<i>P. tremuloides</i>	69	Alberta 50°N	(l) 1734	14	3.1	11	36	5.7	Cragg et al., 1977
	"	"	(o) 3176	25	4.7	16	46	7.0	"
	"	"	(t) 4206	40	7.1	31	55	9.3	"
<i>P. tremuloides</i> ^b		Alberta 51°N	(l) 2500	28	5.3	20	56	6.1	Lousier and Parkinson, 1976
<i>P. tremula</i>	10	USSR 52°N	(l) ^c 3851	42	4.7	61	89	9.3	Remezov and Bykova, 1953
	25	"	(l) ^c 4109	53	4.5	57	76	8.6	"
	50	"	(l) ^c 4880	46	4.2	81	100	9.1	"
<i>P. deltoides</i> (300x300) ^d	1	Mississippi 33°N	(l) 450	6	0.5	4	11	1.9	Baker and Blackmon, 1977
<i>P. x europ.</i> 'I-214'	1	Italy 45°N	(l) 4496	75	6.1	82			Frison, 1975a
<i>P. x europ.</i> 'I-214'	1	Italy 42°N	(l) 2712	33	2.8	28	70		Giulimondi, 1970
<i>P. x europ.</i> 'I-214'	2	"	(l) 6151	98	7.2	79	151		"
<i>P. x europ.</i> 'I-476'	5	Italy 42°N	(l) 7252	125	7.2	98	248	25.4	Duranti and Giulimondi, 1980
	10-13 ^e	"	(l) 5377	89	7.2	75	147	21.3	"
	"	"	(b) 552	2	2.9	2	7	0.6	"
	"	"	(o) 5929	91	10.1	77	154	21.9	"
	"	"	(t) 7136	117	18.0	128	172	25.3	"
Temperate deciduous (ave., 14 sites)	30-120	Europe and N.America (35°N-56°N)	(o) 5399	51	3.6	20	52	6.2	Cole and Rapp, 1981

^a (l) = leaf; (b) = branch; (o) = overstory; (t) = total, including understory^b With admixture of *P. balsamifera* and coniferous species ^c Contains twig fragments ^d Spacing (cm) ^e Average for the years indicated

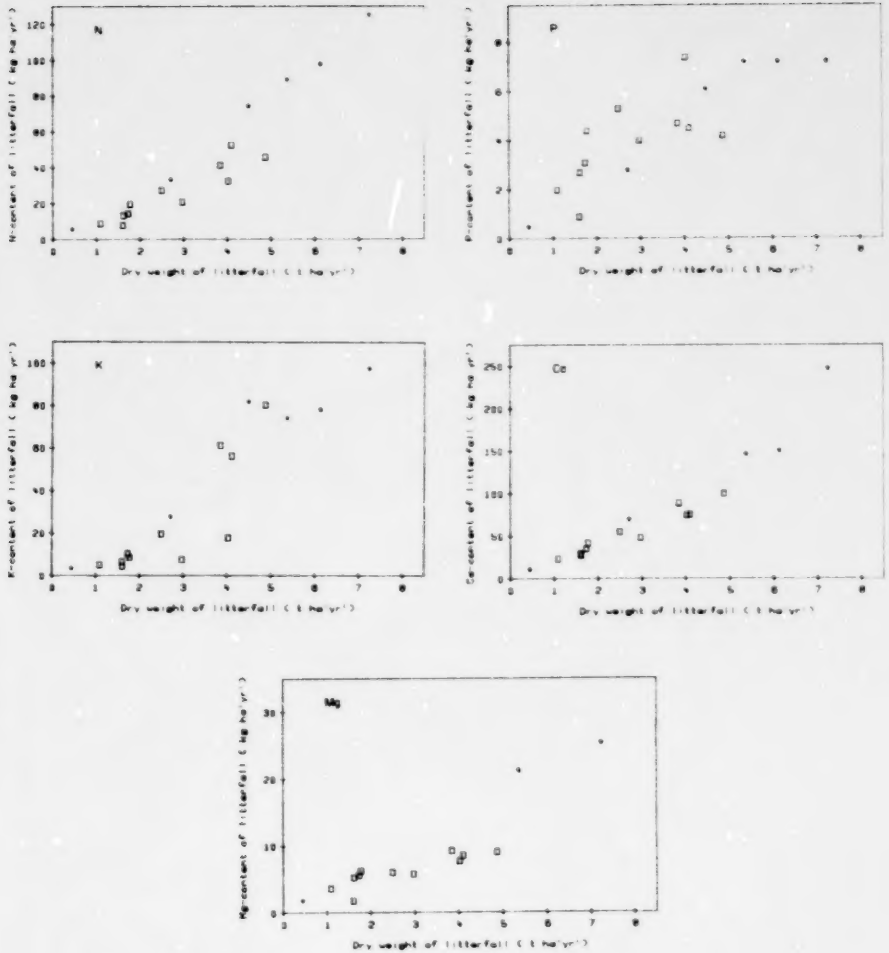


Figure 3. Relationships between nutrient content of *Populus* litterfall and dry weight of litterfall (data from Table 9). □ Leuce, * Algeiros.

Table 10. Nutrient concentrations in freshly fallen leaf litter of Aigeiros and Leuce poplars compared to that of overstory litterfall of 18P sites of temperate deciduous and coniferous forests

Vegetation	No. of sites	Nutrient (kg t ⁻¹)				Reference
		N	P	K	Ca	Mg
Aigeiros poplars	4 ^a	15.9 ^b (0.8)	1.18 (0.06)	13.2 (2.1)	27.2 (1.9)	4.1 (0.1)
Leuce poplars	13	8.9 (0.6)	1.40 (0.16)	7.1 (1.4)	20.3 (0.9)	3.0 (0.5)
Temperate deciduous ^c	14	10.3 (0.9)	0.72 (0.07)	4.0 (0.2)	10.5 (1.6)	1.2 (0.2)
Temperate coniferous ^c	13	8.3 (1.0)	0.83 (0.10)	2.1 (0.3)	6.3 (0.6)	0.94 (0.1)

^a The number of sites is 3 for Ca and 2 for Mg

^b Mean (SEE in parentheses); differences between means of Aigeiros and Leuce poplars are significant (P > 0.05) for N, P, and Ca; for K and Mg the differences between Aigeiros and *P. tremuloides* (9 out of the 13 sites of Leuce poplars: References 2,3,4,5,9,11,12) are also significant (P > 0.05)

^c Includes undefined proportion of branch litter and therefore underestimates concentrations

1. Baker and Blackmon, 1977
2. Bartos and DeSyle, 1981
3. Chandler, 1961
4. Cragg et al., 1977
5. Deaubemire, 1953
6. Duranti and Giulimondi, 1980
7. Frison, 1975a
8. Giulimondi, 1970
9. Lousier and Parkinson, 1976
10. Remesov and Bykova, 1953
11. Van Cleve and Noonan, 1975
12. Verry and Timmons, 1976
13. Viro, 1955

Nutrient release from the forest floor. Available data on forest floor accumulation and on nutrient release from decomposing litter of *Populus* deal primarily with Leuce poplars in cool-temperate and boreal regions (Table 11 and 12). Because climate influences litter decay rate, forest floor accumulation is enhanced in these regions and nutrient pool sizes generally reflect organic matter accumulation (Table 11). The Ca content in the forest floor of *P. tremuloides* is generally higher than that of other boreal and cool-temperate deciduous forests (Cole and Rapp, 1981; Gosz *et al.*, 1976) and reflects the comparatively large Ca fluxes in *Populus* litterfall (Alban *et al.*, 1978; Perala and Alban, 1982b; Van Cleve and Noonan, 1975).

Leaf litter of poplars is rich in nutrients (Table 10), particularly Ca and N. The lignin : nitrogen ratio, a good predictor of litter decay rate (Aber and Melillo, 1982; Melillo *et al.*, 1982), is low; reported values range from 14 for *P. x euram.* 'I-214' (Giulimondi, 1968) to 24 for *P. tremuloides* (Coldwell and DeLong, 1950). Thus, given favorable environmental conditions, leaf litter of *Populus* should decay quickly.

Under the cool and relatively dry conditions of interior Alaska, the turnover time of nutrients in the forest floor of *P. tremuloides* stands varies from 7 to 29 years, which is much longer than the estimated 1- to 6-year average of temperate deciduous forests (Table 12). Leaf litter of *Populus*, as that of other deciduous species, has a highly leachable and labile fraction and loses up to 40% of its initial dry weight within 8-12 months of litter fall (Bartos and DeByle, 1981; Coldwell and DeLong, 1950; Lousier and Parkinson, 1976; MacLean and Wein, 1978; Van Cleve, 1971). Release of nutrients may follow a similar course as dry weight, but patterns of release vary by nutrient, litter characteristics and sites (Perala and Alban, 1982b). The turnover time is consistently the shortest for K and the longest for N.

Environmental conditions in temperate or Mediterranean climates are far more conducive to litter decomposition than the above-mentioned conditions of cool-temperate and boreal regions. Periodic working of soil and irrigation in plantations of *Populus* further enhance litter decomposition (Giulimondi, 1968). Under such conditions the turnover of nutrients is probably well advanced within a year or two (Jensen, 1974; Swift *et al.*, 1979; Williams and Gray, 1974), but this is an area where more research is needed.

2.5 Overall Aspects of Nutrient Cycling

Populus stands and plantations are characterized by higher rates of nutrient acquisition, accumulation and return than most temperate forests, either deciduous or coniferous. These high rates of nutrient cycling relate to the higher growth rate of *Populus* and its higher nutrient requirements. However, large portions of nutrients used in growth annually are periodically involved in cycling, thus allowing the same unit of an element to be used in growth perhaps several times during a rotation, depending on the rate and efficiency of cycling.

Table 11. Reported average organic matter and nutrient contents of the forest floor under *Populus tremuloides*

Location	Stand age (yr)	Organic matter (t ha ⁻¹)	Nutrient (kg ha ⁻¹)				Reference
			N	P	K	Mg	
Alaska (ca 65°N)	10	5.1	89	7	8	575	8 Van Cleve and Noonan, 1975
Minnesota ^a (47°20'N)	40	26.8	667	60	78	1081	89 Perala and Alban, 1982b
	49	22.9	467	38	51	586	64 "
Alaska (ca 65°N)	50	38.3	761	81	88	680	108 Van Cleve and Noonan, 1975
Alberta ^b (50°02'N)	69	66.1	1987	118	272	2575	129 Cragg et al., 1977

^a 40-yr-old stand on loam, 49-yr-old stand on sand

^b With admixture of *P. balsamifera* and coniferous species

Table 12. Reported turnover times for organic matter (O.M.) and nutrients in the forest floor of *Populus tremuloides* in Alaska compared to mean turnover times reported for IBP sites of temperate deciduous forests

Community	Location	Stand age (yr)	Turnover time (yr)					Reference	
			O.M.	N	P	K	Ca Mg		
<i>P. tremuloides</i>	Alaska (ca 65°N)	50	13.0	28.6	10.7	6.9	8.0	8.7	Van Cleve and Noonan, 1975
		120	12.6	30.0	10.9	9.7	10.1	10.7	
Temperate deciduous (ave. 14 sites)	Europe and N. America (35°N - 56°N)	30-140	4.0	5.5	5.8	1.3	3.0	3.4	Cole and Rapp, 1981

Rate of cycling. Cycling rates are dependent on the processes regulating nutrient flows i.e. uptake, translocation, return, and release of nutrients bound in the forest floor. These, in turn, are strongly influenced by the inherent growth rate of species and clones and by environmental conditions of growth. Therefore, it comes as no surprise that the highest rates of cycling in *Populus* were reported for fast-growing euramerican hybrid poplars in the Mediterranean region.

Rates of cycling also vary as the stand develops (Miller, 1981). Nutrient requirements are maximal in the early formative period of the stand and rates of cycling are expected to vary during these years; some stability is reached only when the foliar mass stabilizes (Miller, 1981, 1982). Much of the cycling efficiency of internally-cycled nutrients is related to the age of the plantation or stand, and this is of considerable practical importance for management purposes.

Efficiency of cycling. Cycling efficiency may be expressed by the proportion of total nutrient requirements involved in cycles, i.e. not retained in perennial tissues over the years (Table 13). For nutrients involved in biochemical cycling (essentially N and P), efficiency of cycling increases markedly with age of plantation. By contrast, efficiency of cycling of the base elements appears little affected by age. It should be noted that the method of calculation of total requirement of an element based, in part, on its net increase in woody tissues, underestimates both the requirement and the contribution from internal cycling in the stem (Miller, 1982). However, this does not apply to Ca, whose rate of accumulation in stems and branches of *Populus* closely follows dry-weight accumulation. Therefore, Ca is the cation perhaps least efficiently cycled over the years. Bark of poplar is the depository of about half of the accumulated Ca in stem and branches (Alban *et al.*, 1978; Frison, 1969b; Shelton *et al.*, 1982; Switzer *et al.*, 1976).

Internal cycling increases nutrient-use efficiency, reduces the stand's dependence upon uptake and minimizes potential losses by deep percolation (Bormann *et al.*, 1977; Ostman and Weaver, 1982; Ryan and Bormann, 1982; Shelton *et al.*, 1982). Available data on *Populus* suggest that the turnover of P is slower than that of N (Table 13). This may relate to the fate of P during translocation from senescing foliage and reflect the characteristic storage and recovery process of this element within the trees. There is evidence that, in *Populus*, a significant proportion of otherwise retained P in wood might be recovered only when sapwood is actively transformed into heartwood (Clément and Janin, 1976). More research is needed to assess the extent to which P may be recovered through this pathway in *Populus*.

Euramerican hybrid poplars in the Mediterranean region appear to be translocating a lesser proportion of the N from senescing foliage than do other poplar species in other regions. The origin of this difference is unclear and may be related to several factors (Chapin and Kedrowski, 1983; Ostman and Weaver, 1982; Stachurski and Zimka, 1975; Turner, 1977; Vitousek, 1982).

Table 13. Cycling of nutrients in *Populus*, expressed as a percent of aboveground nutrient requirements (calculated from authors' data)

Species or clone	Age (yr)	Percent cycled						Reference
		N	P	K	Ca	Mg		
<i>P. deltoides</i>	1	53	40	67	67	70	Baker and Blackmon, 1977	
	16 ^a	78	65	67	63	68	Shelton et al., 1982	
<i>P. x eurum.</i> 'I-214'	1	45	31	64			Frison, 1975a	
	13 ^b	72	56	62	67		Frison, 1969b	

^a Requirement is for standing crop, three thinnings and cumulative mortality

^b Requirement based on foliage production and net increase in stem and branches

3. CONSEQUENCES FOR MANAGEMENT

Yield, nutrient requirement and cycling. High yields of biomass are coupled with high rates of nutrient accumulation. Closely-spaced plantations which maximize production also maximize nutrient requirements and uptake. Nitrogen requirements may reach 100-250 kg ha⁻¹yr⁻¹, depending on the clone and density of planting.

High growth performances of *Populus* involve large amounts of base nutrients and consequently are only possible in soils with a high base status. On such soils, and provided moisture is adequate, it may be expected that yields will probably follow N and P status. This is supported by the results of fertilizer applications showing that, in most cases, positive growth response is limited to N and P applications (Barnéoud and Bonduelle, 1979; Blackmon, 1976, 1977b; Frison, 1978; Garbaye, 1980; Ménétrier and Vallée, 1960).

Significant proportions of the nutrients used in growth are periodically cycled, but the extent of cycling is a function of elements and of rotation length. About two-thirds of the K, Ca and Mg requirements are expected to return to soil annually with the litterfall or the associated throughfall. The return of N and P may be only 35-40% of the requirement because substantial amounts of these nutrients are withdrawn from senescing foliage and cycled internally. The contribution of internal cycling to the requirements of N and P in the first years of the stand lags behind the contribution in closed-canopy stands, partly because the weight of new foliage at any one year exceeds the weight formed the previous years (Miller, 1981). Another time-related factor is the internal cycling in stem and branches which is reflected in concentration decreases. Shorter rotations, therefore, rely more heavily on uptake from soil than do longer rotations.

Nutrient cost of harvest. The nutrient cost of harvesting (or the gross nutrient concentration), i.e. the amount of a nutrient harvested per unit dry weight of harvested stems and branches, is an important management consideration (Crane *et al.*, 1981).

Nutrient cost of harvesting *Populus* decreases progressively with age until 8-10 years and subsequently remains relatively constant (Figure 2). Calcium cost appears to be independent of age. Harvesting before 8-10 years may increase nutrient cost dramatically, particularly for N and P. Amounts of nutrients removed after age 8-10 seem to be directly related to dry weight of stems and branches harvested, at least in non-luxury supply conditions of nutrients.

Because Leuce poplars are less site-demanding than poplars of other sections and hybrid poplars in general, they may be considered more efficient in terms of biomass production per unit elemental drain (Anderson, 1979). Present available information is too limited to reach a firm conclusion, but it rather suggests that Aigeiros poplars, including the highly demanding euramerican hybrids, do not accumulate more nutrients per unit weight of stems and branches than the Leuce poplars for which data are available. This is in spite of considerable differences in growth rate and in environmental conditions of growth. But more information on nutrient accumulation in Leuce as well as Tacamahaca poplars is needed and this appears an important area for future research.

By comparison with species of temperate deciduous forests, *Populus* seems to have lower N concentrations, but higher concentrations of the other major nutrients, especially P (Table 14). For the base elements, this difference may relate to the high base status of soils on which poplars grow; it also reflects the high requirements poplars have for these elements in order to perform well in growth.

Nutrient balance and maintenance of productivity. Maintaining nutrient balances in sites managed for frequent harvesting is a basic consideration if site productivity is to be preserved. The influence of yield, harvesting intensity and rotation length, as factors influencing the potential for soil depletion in harvesting poplars, has been discussed extensively (Baker, 1978; Boyle, 1975, 1976; Hansen and Baker, 1979; Switzer and Nelson, 1973; Wells, 1981; White, 1974). The impact of nutrient export and losses from a given site depends on the size of soil available nutrient reserves and on the rate of replenishment of these pools by natural processes of input. But the lack of site-specific information on these processes, particularly the release rate of nutrients by mineral weathering and leaching losses, may limit the forest manager's ability to make reliable estimates of nutrient budgets (Alban, 1979). However, information from several sources shows that, in undisturbed forests, output of bases consistently exceeds input, whereas the efficient cycling processes of N and P provides for their retention in the forest system (Table 15; Bormann *et al.*, 1977; Henderson *et al.*, 1978).

For plantations of *P. deltoides* on alluvial soils of the lower Mississippi Valley, the potential for soil depletion (net uptake minus atmospheric input as a percentage of the soil N and available nutrients)

Table 14. Gross concentration of nutrients in stem and branches of *Populus* stands compared to that of stands of other tree genera and locations

Vegetation and location	Age (yr)	Nutrient (kg c ⁻¹)					Reference
		N	P	K	Ca	Mg	
<i>Populus</i>							
USA and Italy	12- 49	1.72- 1.91	0.23- 0.37	1.24- 2.21	4.00- 5.79	0.32- 0.47	From Figure 2a
<i>Betula</i>							
Finland	40	1.65	0.18	0.95	1.66		From Mäkiläinen, 1977
Alaska	50	1.79	0.15	0.86	1.57	0.31	From Cole and Rapp, 1981b
<i>Fagus</i>							
Germany	59	2.05	0.30	0.68	2.04	0.25	From Cole and Rapp, 1981b
Sweden (3 sites)	90-100	1.11- 1.21	0.15- 0.25	1.34- 1.36	1.82- 2.80	0.31- 0.36	From Mithgaard and Lindgren, 1977
<i>Quercus</i>							
Tennessee	30- 80	2.44	0.16	1.44	6.01	0.25	From Cole and Rapp, 1981b
Belgium	115-160	2.23	0.14	1.24	3.84	0.29	"
Temperate deciduous (ave., 14 sites)	30-120	2.42	0.18	1.25	3.50	0.34	From Cole and Rapp, 1981

a Alban *et al.*, 1978; Frison, 1969b, 1978; Peralta and Alban, 1982a; Schmidt *et al.*, 1981; Switzer *et al.*, 1976

b Values quoted by Cole and Rapp from work of Van Cleve; Ulrich, Eilenberg; Harris, Henderson; Duvigneaud and Denayer-DeSmet

Table 15. Average annual atmospheric inputs, outputs, and net gain or loss of elements from several temperate forest ecosystems (Ralston, 1978)

Element	Environment	No. observ.	Input	Output	Net gain or loss	Range in net gain or loss	
					kg ha ⁻¹ yr ⁻¹		
N	Variable	15	7.9	2.0	5.9	17.5 ^b	to 0.5
P	Variable	16	0.26	0.15	0.11	0.52	to -0.2
K	Inland	12	1.6	3.5	- 1.9	-0.1	to -5
	Oceanic	7	2.6	5.5	- 2.9	0.7	to -8
Ca	Acid	15	4.4	11.4	- 7.0	-0.1	to -20
	Calcareous ^a	4	10.5	102.9	-92.4	-44.8	to -137
Mg	Acid	15	2.0	5.7	- 4.2	-1.5	to 7.4
	Calcareous	3	2.2	40.8	-38.6	-7.4	to -75

^a Includes carbonates and mafic parent materials

^b Includes atmospheric N fixation

was estimated to be less than 0.5% per decade for all elements but K, except for whole-tree harvest in short (9-year) rotation (Shelton *et al.*, 1982). On the basis of the slowly-available pool size and release properties of the soil K, the potential for soil depletion was judged small in these systems, particularly under conservative utilization practices.

For plantations of euramerican hybrid poplars on typical alluvial sandy soils in Italy, Frison (1978) estimated that, on the basis of harvesting 90 t ha⁻¹ of stem and branches in 10- to 13-year rotations, net removal of nutrients averaged 163 kg N, 33 kg P, 199 kg K and 414 kg Ca per hectare. It was felt that sites not subject to recurrent flooding might eventually require the addition of fertilizers to maintain productivity.

These observations seem to support the commonly held view that, on good sites and for sufficiently long rotations with conservative practices, nutrient output is probably balanced by input from natural processes (Ballard, 1979; Switzer *et al.*, 1978; Wells, 1981).

Using the regression models in Figure 2, estimates of nutrient removal were made for a 8 t ha⁻¹yr⁻¹ yield (Table 16), assuming that the same annual production may be obtained over a wide range of combinations of rotation length and spacing (Cannell, 1980; Heilman and Peabody, 1981; Krinard and Johnson, 1980). These estimates show that, for the same intensity of harvest, 4-year rotations would remove approximately twice as much N and P, and 1.5 times as much K and Mg as 12-year rotations, and that some 40 kg Ca ha⁻¹yr⁻¹ would be removed at harvest, irrespective of rotation length.

Table 16. Simulated annual nutrient removal in harvesting *Populus* for a mean annual increment of 8 t ha⁻¹yr⁻¹ of stem and branches over different rotation lengths (Concentration values from Figure 2)

Element	Removal (kg ha ⁻¹ yr ⁻¹) by length of rotation (yr)			
	4	8	12	16
N	30	20	16	14
P	4.7	3.3	2.7	2.4
K	21	17	15	14
Ca ^a	43	43	43	43
Mg	6.1	4.7	4.0	3.7

^a Because Ca concentration is independent of age, the mean value of data presented in Figure 2 (i.e. 5.4 kg t⁻¹) was used (standard deviation: ± 0.9 kg t⁻¹)

Table 17. Range of reported inputs of atmospheric nutrients (Miller, 1982)

	Nutrient (kg ha ⁻¹ yr ⁻¹)				
	N	P	K	Ca	Mg
Bulk precipitation:					
European reports	1-22	0.02-0.50	0.5-20.0	1.0-20.0	0.5- 7.0
North American reports	2- 9	0.07-2.30	0.2- 3.0	0.4-10.0	0.1-13.0
Trapped aerosol and dust	0- 4	0-0.2	4- 6	4-6	0.5- 2.0

Estimated annual N removals in rotations shorter than 12 years would probably be in excess of meteorologic inputs in most sites (Table 17). The system's ability to close the gap, without any significant long term reduction in the site's N reserve, is largely dependent on how much N is added through biological fixation, a process on which quantitative information is scarce.

Current estimates of P input from precipitation and mineral weathering are in the range of $1.1 - 2.2 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Wood *et al.*, 1977), which is well below the estimated annual removal of high yield poplar production in short rotation (Table 16). This suggests potential problems of maintaining site productivity in soils relatively low in P, if no other sources of input are involved.

Irrespective of rotation length, simulated removals of the base elements (Table 16), except perhaps for Mg, are probably beyond atmospheric (Tables 15 and 17) and weathering (Clayton, 1979) inputs on a wide variety of sites. The pool size of the slowly available soil K has been emphasized in plantation nutrition and may considerably influence the K budget of a plantation (Shelton *et al.*, 1982). For Ca, the simulated annual removal of $43 \text{ kg ha}^{-1} \text{ yr}^{-1}$ illustrates the magnitude of harvest export that can be expected for this element. Poplars are widely planted on deep, slightly calcareous soils, and it is generally agreed that, on such sites, the potential for Ca depletion may be negligible, even for nursery production (Giulimondi, 1970). However, Boyle (1975, 1976), Alban (1977) and Alban *et al.* (1978) drew attention to the possible depletion of soil Ca under *P. tremuloides* in the Lake States, because of the large accumulation of this element in aspen in comparison to many other crops, and in view of the relatively low inherent fertility of many sites.

Clearly, poplar production has the potential to remove large quantities of nutrients from sites. Shortening the rotation increases the removal rate of most elements and thus increases the potential for reducing long-term nutrient supply. Plantation sites which are subject to periodic accretion of alluvial input are generally capable of maintaining a high level of productivity without supplemental nutrition (Frison, 1975b; Switzer and Nelson, 1973). In many other sites though, moderate applications of fertilizer N, P, and K is a common practice at establishment or during the development stage of the plantation, a period when tree nutrition is very dependent on soil supplies. While strategies to maintain productivity include fertilization, it should be stressed that replenishment of losses must take into account the low efficiency of fertilizer use by trees (Aber *et al.*, 1982; Ballard, 1979; Bengtson, 1978; Carlisle and Methven, 1979; Switzer *et al.*, 1978) and the nutrient loss by other pathways than removal in wood products (Bormann *et al.*, 1977; Switzer *et al.*, 1978). Thus emphasis should be on preserving rather than restoring productivity (Bengtson, 1978; Wells and Jorgensen, 1979). Biological means of improving nutrition (Fortin *et al.*, 1982; Kormanik, 1979) offer promising ways to help optimize yield while preserving inherent site productivity.

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5. REFERENCES

- Aber, J.D., and J.M. Melillo. 1982. Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. *Can. J. Bot.* 60: 2263-2269.
- Aber, J.D., J.M. Melillo and C.A. Federer. 1982. Predicting the effects of rotation length, harvest intensity and fertilization on fiber yield from northern hardwood forests in New England. *Forest Sci.* 28: 31-45.
- Adams, P.W. 1980. Forest soil and site productivity considerations in northern lower Michigan. Ph.D. Thesis, University of Michigan, Univ. Microfilms, Ann Arbor, Mich.
- Alban, D.H. 1977. The effects of timber harvesting on the soil chemical resource. p. 238-243. In: *Proc. Soc. Amer. Forest.*, Albuquerque, New Mexico.
- Alban, D.H. 1979. Species influence on nutrients in vegetation and soils. p. 152-171. In: *Proc. Impact of Intensive Harvesting on Forest Nutrient Cycling*. College of Environmental Sciences and Forestry, Syracuse, N.Y.
- Alban, D.H., D.A. Perala and B.E. Schlaegel. 1978. Biomass and nutrient distribution in aspen, pine, and spruce stands on the same soil type in Minnesota. *Can. J. For. Res.* 8: 290-299.
- Anderson, H.W. 1979. Biomass production of hybrid poplar grown in mini-rotation. p. 1-13 (XI). In: D.C.F. Fayle, L. Zsuffa and H.W. Anderson (eds.), *Poplar Research, Management and Utilization in Canada*. *Proc. North. Amer. Poplar Council Ann. Meet.* 1977, *For. Res. Inf. Rep.* No. 102.
- Attiwill, P.M. 1979. Nutrient cycling in a *Eucalyptus obliqua* (L'Hérit.) forest. III. Growth, biomass and net primary production. *Aust. J. Bot.* 27: 439-458.
- Attiwill, P.M. 1980. Nutrient cycling in a *Eucalyptus obliqua* (L'Hérit.) forest. IV. Nutrient uptake and nutrient return. *Aust. J. Bot.* 28: 199-222.
- Attiwill, P.M. 1981. Energy, nutrient flow, and biomass. p. 131-144. In: *Proc. Austral. Forest Nutri. Worksh. Productivity in Perpetuity*. CSIRO, Canberra, Australia.
- Baker, J.B. 1978. Nutrient drain associated with hardwood plantation culture. p. 48-53. In: *Proc. 2nd Symp. Southeast. Hardwoods*.
- Baker, J.B., and B. Blackmon. 1977. Biomass and nutrient accumulation in a cottonwood plantation - the first growing season. *Soil Sci. Soc. Amer. J.* 41: 632-636.
- Baker, J.B., and W.M. Broadfoot. 1976. Soil requirements and site selection for Aigeiros poplar plantations. p. 328-343. In: B.A. Thielges and S.B. Land Jr. (eds.). *Proc. Symp. Eastern Cottonwood and Related Species*. Greenville, MS.
- Baker, J.B., and W.K. Randall. 1975. Foliar nitrogen and potassium variation in cottonwood as affected by genetic and site factors. p. 106-111. In: *Proc. 9th Cent. States For. Tree Improv. Conf.* 1974.

- Baker, T.G., and P.M. Attiwill. 1981. Nitrogen in Australian eucalypt forest. p. 159-172. In: Proc. Austral. Forest Nutri. Worksh. *Productivity in Perpetuity*. CSIRO, Canberra, Australia.
- Ballard, R. 1979. Use of fertilizer to maintain productivity of intensively managed forest plantations. p. 321-342. In: Proc. Impact of Intensive Harvesting on Forest Nutrient Cycling. College of Environmental Sciences and Forestry, Syracuse, N.Y.
- Bamber, R.K. 1976. Heartwood, its function and formation. Wood Sci. Technol. 10: 1-8.
- Bard, G.E. 1946. The mineral nutrient content of the foliage of forest trees on three soil types of varying limestone content. Soil Sci. Soc. Amer. Proc. 10: 419-422.
- Barnéoud, C., and P. Bonduelle. 1979. La Culture du Peuplier. AFOCEL, Paris.
- Bartos, D.L., and N.V. DeByle. 1981. Quantity, decomposition, and nutrient dynamics of aspen litterfall in Utah. Forest Sci. 27: 381-390.
- Bartos, D.L., and R.S. Johnston, 1978. Biomass and nutrient content of quaking aspen at two sites in the western United States. Forest Sci. 24: 273-280
- Bengtson, G.W. 1978. Strategies for maintaining forest productivity: a researcher's perspective. p. 123-159. In: T. Tippin (ed.). Proc. Symp. Principles Maintaining Productivity on Prepared Sites. U.S. For. Serv. Southeastern Area State and Private Forestry, Atlanta, GA.
- Blackmon, B.G. 1976. Response of Aigeiros poplars to soil amelioration. p. 344-358. In: B.A. Thielges and S.B. Land Jr. (eds.). Proc. Symp. Eastern Cottonwood and Related Species, Greenville, MS.
- Blackmon, B.G. 1977a. Cottonwood response to nitrogen related to plantation age and site. USDA For. Serv. Res. Note SO-229.
- Blackmon, B.G. 1977b. Effects of fertilizer nitrogen on tree growth, foliar nitrogen and herbage in eastern cottonwood plantations. Soil Sci. Soc. Amer. J. 41: 992-995.
- Blackmon, B.G., J.B. Baker and D.T. Cooper. 1979. Nutrient use by three geographic sources of eastern cottonwood. Can. J. For. Res. 9: 532-534.
- Bonduelle, P. 1979. Production de biomasse par les taillis de salicacées. Ann. AFOCEL, Paris, p. 77-132.
- Bormann, F.H., G.E. Likens and J.M. Melillo. 1977. Nitrogen budget for an aggrading northern hardwood forest ecosystem. Science 196: 981-983.
- Boyle, J.R. 1975. Nutrients in relation to intensive culture of forest crops. Iowa Sta. J. Res. 49: 297-303.
- Boyle, J.R. 1976. A system for evaluating potential impacts of whole-tree harvesting on site quality. TAPPI 59: 79-81.
- Bray, J.R., and E. Gorham. 1964. Litter production in forests of the world. Adv. Ecol. Res. 2: 101-157.
- Brinson, M.M., H.D. Bradshaw, R.N. Holmes and J.B. Elkins, Jr. 1980. Litter-fall, stemflow and throughfall nutrient fluxes in an alluvial swamp forest. Ecology 61: 827-835.

- Broadfoot, W.M., and R.E. Farmer. 1969. Genotype and moisture supply influence nutrient content of eastern cottonwood foliage. *For. Sci.* 15: 46-48.
- Cannell, M.G.R. 1980. Productivity of closely-spaced young poplar on agricultural soils in Britain. *Forestry* 53: 1-21.
- Cannell, M.G.R., and R.I. Smith. 1980. Yields of minirotation closely spaced hardwoods in temperate regions: review and appraisal. *Forest Sci.* 26: 415-428.
- Carlisle, A., and I.R. Methven. 1979. The environmental consequences of intensive forestry and the removal of whole trees. p. 108-120. In: S.G. Boyce (ed.). *Proc. Int. Workshop "Biological and Sociological Basis for a Rational Use of Forest Resources for Energy and Organics"*. MAB-UNESCO, Mich. Sta. Univ., East Lansing, Mich.
- Carter, M.C., and E.H. White. 1971. Dry weight and nutrient accumulation in young stands of cottonwood (*Populus deltoides* Bartr.). *Ala. Agric. Exp. Sta., Auburn Univ., Cir.* 190, Auburn, Ala.
- Chandler, R.F. 1941. The amount and mineral nutrient content of freshly fallen leaf litter in the hardwood forest of central New York. *J. Amer. Soc. Agron.* 33: 859-871.
- Chapin, F.S. III. 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* 11: 233-260.
- Chapin, F.S. III, D.A. Johnson and J.D. McKendrick. 1980. Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: implication for herbivory. *J. Ecol.* 68: 189-209.
- Chapin, F.S. III, and R.A. Kedrowski. 1983. Seasonal changes in nitrogen and phosphorus fractions and autumn retranslocation in evergreen and deciduous taiga trees. *Ecology* 64: 376-391.
- Clayton, J.L. 1979. Nutrient supply to soil by rock weathering. p. 75-96. In: *Proc. Impact of Intensive Harvesting on Forest Nutrient Cycling*. College of Environmental Sciences and Forestry, Syracuse, N.Y.
- Clément, A., and G. Janin. 1973. Étude complémentaire de la présence de cristaux de carbonate de Ca dans le bois des peupliers. Existence de 5 zones fonctionnelles reconnues à partir de leur teneur en phosphore. *Ann. Sci. Forest.* 30: 63-81.
- Clément, A., and G. Janin. 1976. Étude comparée de la répartition des principaux cations et du phosphore dans une tige de peuplier 'Fritzi-Pauley'. *Plant Soil* 45: 543-554.
- Coldwell, B.B., and W.A. DeLong. 1950. Studies of the composition of deciduous forest tree leaves before and after partial decomposition. *Sci. Agric.* 30: 456-466.
- Cole, D.W. 1981. Nutrient cycling in world forests. *Proc. 17th IUFRO World Congress, Japan. Div. 1:* 139-160.
- Cole, D.W., and M.R. Rapp. 1981. Elemental cycling in forest ecosystems. p. 341-409. In: D. Reichle (ed.). *Dynamic Properties of Forest Ecosystems*, IBP Synthesis, Vol. 23. Cambridge Univ. Press, Cambridge.

- Cowling, E.B., and W. Merrill. 1966. Nitrogen in wood and its role in wood deterioration. *Can. J. Bot.* 44: 1539-1554.
- Cragg, J.B., A. Carter, C. Leischner, E.B. Peterson and G.N. Sykes. 1977. Litterfall and chemical cycling in an aspen (*Populus tremuloides*) woodland ecosystem in the Canadian Rockies. *Pedobiologia* 17: 428-443.
- Crane, W.J.B. 1978. Phosphorus stability in Eucalypt forests. *Aust. For.* 41: 118-126.
- Crane, W.J.B., R.J. Raison, G.H. Nicholls and C.M. Godkin. 1981. The effect of rotational age on the phosphorus requirements of forest plantations. Abst. p. 325. In: *Proc. Austral. Forest Nutri. Worksh. Productivity in Ferpetuity*, CSIRO, Canberra, Australia.
- Deaubemire, R. 1953. Nutrient content of leaf litter of trees in the northern Rocky Mountains. *Ecology* 34: 786-793.
- Doucet, R., and J.M. Veilleux. 1982. Recherche et développement sur le peuplier. XVIII. Résultats quinquennaux de traitements d'éclaircie et de fertilisation dans des peupleraies naturelles de diverses classes d'âge. Min. Énergie et Ressources, Québec, Serv. Rech., Mémoire 76.
- Duranti, G., and G. Giulimondi. 1980. Ricerche sulla produttività di un pioppeto artificiale. III. Apporto al suolo di azoto e di elementi minerali con la lettiera ed il sottobosco erbaceo. *Pubbl. Centro Sperim. Agric. Forest.* 13: 229-238.
- Dzekova, M. 1972. [The drain of soil minerals in the production of poplar plants]. *God. Zborn. Zemj. Sum. Fak. Univ. Skopje (Sum).* 24: 37-46.
- Eaton, J.S., G.E. Likens and F.H. Bormann. 1973. Throughfall and stemflow chemistry in a northern hardwood forest. *J. Ecol.* 61: 495-508.
- Ek, A.R., and D.H. Dawson. 1976. Actual and projected growth and yields of *Populus 'Tristis' 1* under intensive culture. *Can. J. For. Res.* 6: 132-144.
- FAO, 1980. *Peupliers et Saules*. Collection FAO: Forêts, No. 10, Rome.
- Forgeard, F., J.C. Gloaguen and J. Touffet. 1980. Interception des précipitations et apport au sol d'éléments minéraux par les eaux de pluie et les pluviocessivats dans une hêtraie atlantique et dans quelques peuplements résineux en Bretagne. *Ann. Sci. For.* 37: 53-71.
- Fortin, J.A., C. Godbout, P. Normand and M. Lalonde. 1982. Maintaining fertility through nitrogen fixing and mycorrhizal symbioses. p. 13-16. In: *Fourth Bioenergy Conference, Research and Development Seminar*, Winnipeg, Man., March 1982. National Research Council of Canada, Ottawa.
- Foster, N.W., and I.K. Morrison. 1976. Distribution and cycling of nutrients in a natural *Pinus banksiana* ecosystem. *Ecology* 57: 110-120.
- Frison, G. 1967. Asportazioni minerali nel barbatellaio di pioppo. *Cellulosa e Carta* 28: 10-24.
- Frison, G. 1968. Asportazioni minerali nel vivaio di pioppi euroamericani. *Cellulosa e Carta* 19: 27-36.
- Frison, G. 1969a. Alcuni aspetti della nutrizione minerale del pioppo in vivaio: produzione in sostanza secca ed assorbimento di sostanze nutritive. *Cellulosa e Carta* 20: 28-34.

- Frison, G. 1969b. Asportazioni minerali nel pioppeto. *Cellulosa e Carta* 20: 5-12.
- Frison, G. 1973. Mineral fertilizing of poplar on deep, alluvial, sandy soil. *Int. Symp. Forest Fertilization, FAO/IUFRO, Paris*, 8 p.
- Frison, G. 1975a. Ritmo di assorbimento di elementi minerali nutritivi del pioppo in barbatellaio. *Cellulosa e Carta* 26: 25-43.
- Frison, G. 1975b. La concimazione del pioppeto. *De Terra e Vita* 16: 22-23.
- Frison, G. 1978. Risultati di cinque esperienze sulla concimazione minerale del pioppo. *Cellulosa e Carta*. 29: 9-26.
- Frison, G. 1979. Ricerche sulla nutrizione minerale del pioppo per mezzo della diagnostica fogliare (Tecnica di campionamento). *Cellulosa e Carta* 30: 5-32.
- Frison, G., N. Anselmi and A. Boccone. 1982. Research on iron chlorosis of poplars. *FAO Int. Poplar. Commission, Casale Monferrato, Italy*. 54 p.
- Fritzsche, K. 1964. Beziehungen zwischen den Blattspiegelwerten, dem Boden-nährstoffgehalt und dem Wachstum einiger Schwartz-und Balsampappeln. Düngung und Melioration in der Forstwirtschaft. *Deu. Akad. Landwirtschaft-wiss.* 66: 169-192.
- Garbaye, J. 1972. Influence de la date et de la hauteur du prélèvement sur les résultats de l'analyse foliaire chez deux clones de peuplier. *Ann. Sci. For.* 29: 451-463.
- Garbaye, J. 1979. Sol et productivité des peupliers 'I-214' et 'Robusta' en populiculture traditionnelle dans le nord du bassin parisien. *Ann. Sci. For.* 36: 39-58.
- Garbaye, J. 1980. Nutrition minérale et production des peupliers 'Robusta' et 'I-214' en populiculture traditionnelle dans le nord du bassin parisien. *Ann. Sci. For.* 37: 159-172.
- Garbaye, J., and P. LeRoy. 1973. Comportement de onze clones de peupliers dans sept pépinières du nord-est. *Rev. For. Franç.* 25: 299-307.
- Giulimondi, G. 1966a. Contenuti minerali dei pioppi euramericani. *Pubbl. Centro Sper. Agric. Forest.* 7-8: 193-214.
- Giulimondi, G. 1966b. Ricerche sulla nutrizione minerale del pioppo a mezzo dell'analisi fogliare: variazioni dei contenuti minerali in prove di concimazione. *Pubbl. Centro Sper. Agric. Forest.* 7-8: 39-54.
- Giulimondi, G. 1968. Effetti della lettiera di pioppo sul terreno. I. Ricerche in vaso sull'evoluzione del materiale di defogliazione. *Pubbl. Centro Sper. Agric. Forest.* 10: 55-71.
- Giulimondi, G. 1970. Contenuti minerali delle piopelle in vivaio. *Pubbl. Centro Sper. Agric. Forest.* 11: 63-74.
- Giulimondi, G., and G. Duranti. 1974. Ritmo d'incremento in sostanza secca e di utilizzazione in elementi nutritivi del pioppo in vivaio durante il secondo anno. *Cellulosa e Carta* 25: 3-20.

- Gosz, J.R., G.E. Likens and F.H. Bormann. 1976. Organic matter and nutrient dynamics of the forest floor in the Hubbard Brook Forest. *Oecologia* 22: 305-320.
- Gosz, J.R., G.E. Likens, J.S. Eaton and F.H. Bormann. 1975. Leaching of nutrients from leaves of selected tree species in New Hampshire. p. 630-641. *In*: F.G. Howell, J.B. Gentry and M.H. Smith (eds.). Mineral Cycling in Southeastern Ecosystems. ERDA Symp. Series Conf-740513, May 1974; Augusta, Georgia.
- Hansen, E.A. 1976. Determining moisture-nutrient requirements for maximum fiber yield. p. 43-46. *In*: Intensive Plantation Culture: Five Years Research, USDA For. Serv. Gen. Tech. Rep. NC-21.
- Hansen, E.A. 1980. Energy and wood from intensively cultured plantations: research and development program. USDA For. Serv. Gen. Tech. Rep. NC-58.
- Hansen, E.A., and J.B. Baker. 1979. Biomass and nutrient removal in short rotation intensively cultured plantations. p. 130-151. *In*: Proc. Impact of Intensive Harvesting on Forest Nutrient Cycling. College of Environmental Sciences and Forestry, Syracuse, N.Y.
- Hansen, E.A., H.A. McNeel, D.A. Netzer, H.M. Phipps, P.S. Roberts, T.F. Strong, A.N. Tolsted and J. Zavitzkowski. 1979. Short rotation intensive culture practices for northern Wisconsin. p. 47-63. *In*: Proc. 16th Ann. Mee., North Amer. Poplar Council, August 14-17.
- Heilman, P.E., and D.V. Peabody. 1981. Effects of harvest cycle and spacing on productivity of black cottonwood in intensive culture. *Can. J. For. Res.* 11: 118-123.
- Henderson, G.S., W.F. Harris, D.E. Todd and T. Grizzard. 1977. Quantity and chemistry of throughfall as influenced by forest type and season. *J. Ecol.* 65: 365-374.
- Henderson, G.S., W.T. Swank, J.B. Waide and C.C. Grier. 1978. Nutrient budgets of Appalachian and Cascade region watersheds: a comparison. *For. Sci.* 24: 385-397.
- Isebrands, J.G., A.R. Ek and R.S. Meldahl. 1982. Comparison of growth model and harvest yields of short rotation intensively cultured *Populus*: a case study. *Can. J. For. Res.* 12: 58-63.
- James, T.D.W., and D.W. Smith. 1977. Short-term effects of surface fire on the biomass and nutrient standing crop of *Populus tremuloides* in southern Ontario, Canada. *Can. J. For. Res.* 7: 666-679.
- Janin, G., and A. Clément. 1972. Mise en évidence de cristaux de carbonate de calcium dans le bois des peupliers. Conséquences sur la répartition des ions minéraux liée à la duraminisation. *Ann. Sci. For.* 29: 67-105.
- Járo, Z. 1958. Alomennyiségek a magyar erdőkben. Erdészettudományi Közlemények, Sopron 1: 151-162. (*Cited in* Bray and Gorham, 1964).
- Jensen, V. 1974. Decomposition of angiosperm tree leaf litter. p. 69-104. *In*: G.H. Dickinson and G.J.F. Pugh (eds.). Biology of Plant Litter Decomposition. Vol. I. Academic Press, London.

- Kormanik, P.P. 1979. Biological means of improving nutrient uptake in trees. p. 293-311. In: E.D. Ford, D.C. Malcolm and J. Attersson (eds.). The Ecology of Even-Aged Forest Plantations. Proc. Meet. Div. I, IUFRO, Edinburgh, U.K.
- Kramer, P.J., and T.T. Kozlowski. 1979. Physiology of Woody Plants. Academic Press, New York.
- Krinard, R.M., and R.L. Johnson. 1980. Fifteen years of cottonwood plantation growth and yield. Southern J. Appl. For. 4: 180-185.
- Lambert, M.J. 1981. Inorganic constituents in wood and bark in some NSW forest species. For. Comm. N.S.W. Australia, Tech. Pap. No. 31.
- Leech, R.H., and Y.T. Kim. 1981. Foliar analysis and DRIS as a guide to fertilizer amendment in poplar plantations. For. Chron. 57: 17-21.
- Lousier, J.D., and D. Parkinson. 1976. Litter decomposition in a cool temperate deciduous forest. Can. J. Bot. 54: 419-436.
- MacLean, D.A., and R.W. Wein. 1978. Weight loss and nutrient changes in decomposing litter and forest floor material in New Brunswick forest stands. Can. J. Bot. 56: 2730-2749.
- Mahendrappa, M.K. 1974. Chemical composition of stemflow from some eastern Canada tree species. Can. J. For. Res. 4: 1-7.
- Mäliköinen, E. 1977. Annual primary production and nutrient cycle in a birch stand. Commun. Inst. For. Fenn. 91: 1-35.
- Marks, P.L. 1974. The role of pin cherry (*Prunus pennsylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. Ecol. Monog. 44: 73-88.
- Melillo, J.M., J.D. Aber and J.M. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63: 621-626.
- Ménétrier, J., and G. Vallée. 1980. Recherche et développement sur le peuplier. XVI. Résultats d'essai de quarante traitements de fertilisation d'une plantation de boutures. Min. Énergie et Ressources, Serv. Rech., Québec, Mémoire 57.
- Merrill, W., and E.B. Cowling. 1966. Role of nitrogen in wood deterioration: amounts and distribution of nitrogen in tree stems. Can. J. Bot. 44: 1555-1580.
- Miller, H.G. 1981. Nutrient cycles in forest plantations, their change with age and the consequences for fertilizer practice. p. 187-199. In: Proc. Austral. Forest Nutri. Worksh. Productivity in Perpetuity. CSIRO, Canberra, Australia.
- Miller, H.G. 1982. Nutrient cycling in Alder. Silvicultural implications in intensively managed plantations. Int. Energy Agency - Planning Group B JAB-21, Nutrient cycling report, April 1982.
- Mitchell, H.L., and R.F. Chandler. 1939. The nitrogen nutrition and growth of certain deciduous trees of Northeastern United States. Black Rock Forest Bull. 11.

- Nakos, G. 1975. Seasonal changes in foliar nutrient concentrations of forest species in nursery. II. Poplar hybrids. Min. Agric., For. Res. Inst. Athens, No. 74.
- Nihlgard, B., and L. Lindgren. 1977. Plant biomass, primary production and bioelements of three mature beech forests in South Sweden. *Oikos* 28: 95-104.
- Ogar, G.E. 1981. Effects of spacing and NK fertilizers on dry matter accumulation and nutrient contents of two-year-old *Populus x euramericana* cv. I-45/51 and cv. robusta DN 17. ENFOR Project P-121. Ottawa, Canada.
- Ostman, N.L., and G.T. Weaver. 1982. Annual nutrient transfers by retranslocation, leaching and litter fall in a chestnut oak forest in southern Illinois. *Can. J. For. Res.* 12: 40-51.
- Ovington, J.D. 1959. The circulation of minerals in plantations of *Pinus silvestris* L. *Annals Bot.* 23: 229-239.
- Perala, D.A., and D.H. Alban. 1982a. Biomass, nutrient distribution and litterfall in *Populus*, *Pinus* and *Picea* stands on two different soils in Minnesota. *Plant Soil* 64: 177-192.
- Perala, D.A., and D.H. Alban. 1982b. Rates of forest floor decomposition and nutrient turnover in aspen, pine, and spruce stands on two different soils. USDA For. Serv., North Central For. Exp. Sta., Res. Pap. NC-227.
- Raitanen, W.E. 1980. The hybrid poplar program: farming fast growing hardwoods in the eastern Ontario region. Ont. Min. Nat. Resou., Second Western Hemisphere Energy Symposium, Rio de Janeiro, Brazil, Sept. 22-27, 1980.
- Ralston, C.W. 1978. Mineral cycling in forest ecosystems. p. 320-340. In: C.T. Youngberg (ed.). *Forest Soils and Land Use*. Proc. 5th N.A. For. Soils Conf., Fort Collins, Colorado.
- Ranger, J. 1981. Étude de la minéralomasse et du cycle biologique dans deux peuplements de Pin laricio de Corse, dont l'un a été fertilisé à la plantation. *Ann. Sci. For.* 38: 127-158.
- Reiners, W.A. 1972. Nutrient content of canopy throughfall in three Minnesota forests. *Oikos* 23: 14-22.
- Remezov, N.P., and L.N. Bykova. 1953. [Uptake and cycle of N and ash elements in Aspen stands]. *Pochvoved.* 8: 28-41.
- Rodin, L.E., and N.I. Bazilevich. 1967. *Production and Mineral Cycling in Terrestrial Vegetation*. English translation: G.E. Fogg. Oliver and Boyd, Edinburgh and London.
- Rossi Marcelli, A., G. Duranti and G. Giulimondi. 1980. Ricerche sulla produttività di un pioppeto artificiale. II. Produttività primaria netta del pioppeto. *Pubbl. Centro Sper. Agric. For.* 13: 203-227.
- Ryan, D.F., and F.H. Bormann. 1982. Nutrient resorption in northern hardwood forests. *BioScience* 32: 29-32.
- Schmitt, M.D.C., M.M. Czapowskyj, L.O. Safford and A.L. Leaf. 1981. Biomass and elemental uptake in fertilized and unfertilized *Betula papyrifera* Marsh, and *Populus grandidentata* Michx. *Plant Soil* 60: 111-122.

- Schoenfeld, P.H. 1975. A method for site-growth research in a stand of *Populus* cv. 'Gelrica'. Ned. Bosb. Tijdschrift 47: 164-173.
- Sheedy, G., and G. Vallée. 1976. Recherche et développement sur le peuplier dans la région de l'est-du-Québec. IX. Croissance et résistance au gel suite à l'application d'engrais. Min. Terres et Forêts, Québec, Serv. Rech., Mémoire 34.
- Sheedy, G., and G. Vallée. 1981. Recherche et développement sur le peuplier. XVII. Comportement de 15 clones à la suite de l'application de trois traitements de fertilisation. Min. Énergie Ressou., Québec, Serv. Rech., Mémoire 72.
- Shelton, M.G., L.E. Nelson, G.L. Switzer and B.G. Blackmon. 1981. The concentration of nutrients in tissues of plantation-grown eastern cottonwood (*Populus deltoides* Bart.). MS. Agric. For. Exp. Sta. Tech. Bull. 106, Mississippi State, MS.
- Shelton, M.G., G.L. Switzer, L.E. Nelson, J.B. Baker and C.W. Mueller. 1982. The development of cottonwood plantations on alluvial soils. MS. Agric. For. Exp. Sta. Tech. Bull. 113, Mississippi State, MS.
- Smirnov, V.V., and V.G. Semenova. 1972. Seasonal dynamics of ash elements in leaves of birch and aspen. Soviet J. Ecol. 3: 167-168 (English translation, 1973, Consultants Bureau, N.Y.).
- Stachurski, A., and J.R. Ziarka. 1975. Methods of studying forest ecosystems: leaf area, leaf production, and withdrawal of nutrients from leaves of trees. Ekol. Pol. 23: 637-648.
- Sviridova, I.K. 1960. (Pochvovedenie 4: 68-73. Trans. in Soviet Soil Sci. 1961). Role of improvement cuttings in raising forest soil fertility. Soviet Soil Sci. 1: 401-405.
- Swift, M.J., O.W. Heal and J.M. Anderson. 1979. Decomposition in Terrestrial Ecosystems. Studies in Ecology Vol. 5. University of California Press, Berkeley and Los Angeles.
- Switzer, G.L., and L.E. Nelson. 1972. Nutrient accumulation and cycling in loblolly pine (*Pinus taeda* L.) plantation ecosystems: the first twenty years. Soil Sci. Soc. Amer. Proc. 36: 143-147.
- Switzer, G.L., and L.E. Nelson. 1973. Maintenance of productivity under short rotation. p. 365-389. In: Proc. Int. Symp. For. Fert. FAO-IUFRO, Ministère de l'Agriculture, Paris.
- Switzer, G.L., L.E. Nelson and J.B. Baker. 1976. Accumulation and distribution of dry matter and nutrients in Aigeiros poplar plantations. p. 359-369. In: Proc. Symp. East. Cottonwood and Related Species, Greenville, Miss.
- Switzer, G.L., L.E. Nelson and L.E. Hinesley. 1978. Effects of utilization or nutrient regimes and site productivity. p. 91-102. In: C.W. McMillen (ed.). Symp. Complete Tree Util. South. Pine., For. Prod. Res. Soc., Madison Wisc.
- Tew, R.K. 1970. Seasonal variation in the nutrient of aspen foliage. J. Wildl. Manage. 34: 475-478.

- Touzet, G. 1982. Technique et économie de la production de biomasse de salicacées en France. Int. Poplar Commission, Ad-hoc Comm. on Biol. Prod. Syst. in *Salicaceae*, Casale Monferatto, Italy, Sept. 6-10. Mimeo., 11 p.
- Touzet, G. and J.C. Heinrich. 1970. Concentrations foliaires en azote, phosphore, potassium et calcium du peuplier cv. 'I-214'. AFOCEL: 103-134.
- Tukey, H.B. Jr. 1970. The leaching of substances from plants. Ann. Rev. Plant Physiol. 21: 306-324.
- Turner, J. 1977. Effect of nitrogen availability on nitrogen cycling in a Douglas-fir stand. Forest Sci. 23: 307-316.
- Turner, J., and M.J. Lambert. 1981. Nitrogen cycling within a 27-year-old *Eucalyptus grandis* stand. p. 303-310. In: R.A. Rummery and F.J. Hingston (eds.). Managing Nitrogen Economies of Natural and Man Made Forest Ecosystems, CSIRO, Div. Land Resou. Manage., Australia.
- Vallée, G., and E. Chamberland. 1978. Recherche et développement sur le peuplier. XIII. Potentiel de production fourragère et valeur alimentaire de sept clones. Min. Terres et Forêts, Québec, Serv. Rech., Mémoire 48.
- Van Cleve, K. 1971. Energy and weight-loss functions for decomposing foliage of birch and aspen stands in interior Alaska. Ecology 52: 720-723.
- Van Cleve, K., and L.L. Noonan. 1975. Litterfall and nutrient cycling in the forest floor of birch and aspen stands in interior Alaska. Can. J. For. Res. 5: 626-639.
- van den Burg, J. 1977. Growth of Euramerican poplar and N content of soil organic matter. Populier 14: 55-58.
- van den Burg, J. 1980. The influence of pH on the growth and foliar composition of poplar. Populier 17: 27-31.
- van den Burg, J., and P.H. Schoenfeld. 1978. Poplar cultivation, soil fertility and soil chemical analysis. Populier 13: 75-80.
- van der Meiden, H.A., and H.W. Kolster. 1964. Variations in the mineral content of poplar leaves during the vegetation season and in different parts of the plant. Ned. Bosb. Tijdschrift 36: 1-11.
- Verry, E.S., and D.R. Timmons. 1976. Elements in leaves of a trembling aspen clone by crown position and season. Can. J. For. Res. 6: 436-440.
- Verry, E.S., and D.R. Timmons. 1977. Precipitation nutrients in the open and under two forests in Minnesota. Can. J. For. Res. 7: 112-119.
- Viro, P.J. 1955. Investigations of forest litter. Comm. Inst. Forestal. Fenn. 45: 1-65.
- Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. The Amer. Naturalist 119: 553-572.
- Wardell, J.F., and J.H. Hart. 1973. Radial gradients of elements in White Oak wood. Wood Sci. 5: 298-303.
- Wells, C.G. 1981. Nutrient balances and high productivity. p. 439-443. In: Proc. TAPPI Ann. Mee. Chicago. IL. March 2-5, 1981.

- Wells, C.G., and J.R. Jorgensen. 1979. Effect of intensive harvesting on nutrient supply and sustained productivity. p. 212-230. In: Proc. Impact of Intensive Harvesting on Forest Nutrient Cycling. College of Environmental Sciences and Forestry, Syracuse, N.Y.
- White, E.H. 1974. Whole-tree harvesting depletes soil nutrients. Can. J. For. Res. 4: 530-535.
- White, E.H., and M.C. Carter. 1968. Relationships between foliage nutrient levels and growth of young natural stands of *Populus deltoides* Bartr. p. 275-294. In: C.T. Youngberg and C.B. Dovey (eds.). Tree Growth and Forest Soils. Oregon State Univ. Press, Corvallis, OR.
- Williams, S.T., and T.R.G. Gray. 1974. Decomposition of litter on the soil surface. p. 661-668. In: G.H. Dickinson and G.J.F. Pugh (eds.). Biology of Plant Litter Decomposition, Vol. II. Academic Press, London and New York.
- Witkamp, M. and J. van der Drift. 1961. Breakdown of forest litter in relation to environmental factors. Plant Soil 15: 295-311.
- Wood, B.W., R.F. Wittwer and S.B. Carpenter. 1977. Nutrient element accumulation and distribution in an intensively cultured American sycamore plantation. Plant Soil 48: 417-433.
- Zavitkovski, J. 1981a. Structure and seasonal distribution of litterfall in young plantations of *Populus 'Tristis' 1*. Plant Soil 60: 409-422.
- Zavitkovski, J. 1981b. Some promising forest ecosystems of the temperate zone for biomass production and energy storage. p. 129-143. In: J.W. White, W. McGrew and L. Courtney (eds.). Symp. on Energy from Biomass and Wastes. V. Jan. 26-30, 1981, Lake Buena Vista, Fla.
- Zsuffa, L., and H.W. Anderson. 1979. The potential of poplar plantations. Panel 2. In: Int. Symp. For. Sci. and Their Contrib. to Develop. of Trop. America, San Jose, Costa Rica, Oct. 11-17. 12 p.

POOR

QUALITY

ORIGINAL